1992

Comparative ecology of two South American foxes, Dusicyon griseus and D culpaeus

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Comparative ecology of two sympatric South American foxes, *Dusicyon griseus* and *D. culpaeus*

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Iowa State University, 1992

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Comparative ecology of two South American foxes, *Dusicyon griseus* and *D. culpaeus*

by

Warren E. Johnson

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major: Animal Ecology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

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Signature was redacted for privacy.

Iowa State University
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1992

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I am grateful to all who provided assistance during this study. I thank my POS committee, especially Bill Franklin, my major professor, for his support and encouragement, and Bill Clark, for his valuable guidance and insight.

I thank the Chilean National Forestry and Park Service (CONAF) for permitting me to work in their wonderful National Park. I give special thanks to the personnel of Torres del Paine National Park for their help, collaboration and friendship. Park superintendent Guillermo Santana gave timely assistance and support on several occasions. Park guards Oscar Guineo, Francisco Barrientos, and Juan Toro provided invaluable advice, knowledge, and assistance, giving me a more intimate insight into "their park." Gladys Garay and Rosa Abello opened their homes to me with wonderful hospitality and helped nurse me through several rough times.

I appreciate the dedicated field work and initiative of Fredy Barrientos, Gail Blundell, and Judith Hoffman. Gabriel Arribillaga, Jill Bright, Steve Catir, Lloyd Christensen, Gladys Garay, Kyle Harms, Agustin Iriarte, Richard Lawrence, Andy Phillips, Peter Ricci, and Steve Wilson also assisted in the field work. Todd Fuller provided invaluable initial incentive for the project and along with Barry Sampson taught me some of the finer points of the art of trapping. Michael Behl provided important editorial comments, and Kenneth

Koehler gave valuable statistical advice. I also owe thanks to Kurt Johnson, without whose help and initiative this project would never have become a reality.

This study was funded by grants from the National Geographic Society and Patagonia Research Expeditions (Iowa State University) to W. L. Franklin and the Organization of American States to K. A. Johnson and W. L. Franklin. I received additional funding from an International Telephone and Telegraph Corporation Fellowship and the National Wildlife Federation. This project was conducted under a research agreement (Proyecto Puma) between Iowa State University and CONAF.

I value and appreciate the support of my parents, Nancy and Bill, my sister Susan and brother Steven. I especially thank my wife Mariane, for her love, friendship, and understanding, and my son Daniel, for making it so easy for me to share space in my office with a crib, playpen, and toys, and still be productive.

Finally I thank all of the Chileans who befriended me, gave me help throughout my stay in Chile, and made Chile my home away from home. Muchísimas gracias.

GENERAL INTRODUCTION

The organization of animal communities is influenced by many factors and has been of primary interest to ecologists in the last several decades. However, since the seminal paper of Rosenzweig (1966), relatively few studies have attempted to describe and explain carnivore community organization. Of the Carnivora, little is known about the community structure of the Canidae, or dog family, in spite of its wide distribution. Canid habitat selection, resource utilization, and competition are of special interest because foxes, wolves, and dogs exhibit a wide array of behavioral and ecological adaptations, as well as considerable intraspecific variation.

The goal of this dissertation was to review the interactions and ecological relationships of sympatric canids and to discuss the ecological factors promoting sympatry. Specifically, the objectives were to document instances of canid sympatry and to compare several ecological parameters considered to be important in assessing potential competition. Second, the canid community structure in Torres del Paine National Park, Chile was studied in detail by comparing the behavioral ecology of grey and culpeo fox and reviewing factors hypothesized to determine their distribution when sympatric.

Explanation of common and scientific names

Taxonomic classification of the family Canidae is unresolved, especially at the generic and subfamiliar levels. I will use the classification system of Ginsberg and Macdonald (1990), which closely follows that of Clutton-Brock et al. (1976) and Corbet and Hill (1986). These systems place the two species I studied in the genus Dusicyon, along with four other South American canids. Other classification schemes have placed them in the genus Pseudalopex (Berta 1987, Nowak 1991), along with two other South American foxes, or in the genus Canis (Langguth 1975, Van Gelder 1978).

In English D. culpaeus has been called culpeo, culpeo fox, colored fox, large fox, culpaeo fox, colpeo fox, South American red fox, and Andean wolf and in Spanish zorro colorado, zorro culpeo, zorro rojo, zorro grande, lare. English names for D. griseus include Argentine fox, Argentine gray fox, chico gray fox, little gray fox, pampa fox, chilla, and South American gray fox. (Note the British spelling of grey is often used.) Spanish names include zorro gris, zorro chilla, zorro chico, and zorro gris chico. To avoid confusion with the red fox (Vulpes vulpes) or the gray fox (Urocyon cinereoargenteus), I will use culpeo fox and South American grey fox, or for brevity, grey fox.

Explanation of dissertation format

This dissertation is organized under the guidelines for the alternate dissertation format (Iowa State University Graduate College Thesis Manual). I wrote each section under the supervision of Dr. William L. Franklin and my POS committee in the format of a manuscript ready for submittal to a professional journal. Section 1 is written in the format of Conservation Biology, Section 2 of The Journal of Mammalogy, Section 3 of Journal of Animal Ecology, and Section 4 of Oecologia. Because the manuscripts will be submitted with multiple authorship, the personal pronoun "we" is used. Following the last Section there is a General Summary, which is followed by the references cited in the General Introduction and General Summary.

SECTION 1.

CONSERVATION ECOLOGY OF SYMPATRIC CANIDS

Conservation Ecology of Sympatric Canids

Running Head: Sympatric Canid Conservation

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ABSTRACT

Literature on assemblages of coexisting canidae was reviewed to determine the factors promoting sympatry, estimate the conservation implications of species elimination or reintroduction, and suggest foci of future research. The number of sympatric canids per area seems determined by a combination of biogeographical history, human intervention, and environmental diversity and productivity. Temporal activity of all canid species pairs overlaps a medium to high amount. Also, sympatric canids either segregate in different habitats or utilize different food resources, but do not do both. Interactions among sympatric canid species may have important conservation and management implications because the structure of a canid community often changes after a species' range expansion, extirpation, or reintroduction. In addition to much needed descriptive studies of the many little-known canid species, well-designed comparative and experimental studies on sympatric canids are necessary to further elucidate the mechanisms of species coexistence.

INTRODUCTION

The canidae, or dog family, is one of the most widely distributed of the order Carnivora, with members on all continents except Antarctica. Foxes, wolves, and dogs exhibit a wide variety of behavioral and ecological adaptations. Their social systems range from loose pairs to large packs and they are found in almost every habitat from deserts to tropical rain forests and arctic pack ice. Canids demonstrate considerable intraspecific variation; their social structure, habitat use, food habits, body size, and reproductive parameters vary substantially under different ecological conditions (Macdonald 1983, Moehlman 1989). Because many canid species have such flexible socioecologies and similar adaptations to environmental constraints (Bekoff et al. 1981, Bekoff et al. 1984), they are potentially strong competitors, which, in theory, should lead them to partition needed resources.

Differential morphology of sympatric canids has been used to provide evidence for resource partitioning and potential competition. Wayne et al. (1989) demonstrated that, with the exception of the three east African jackal (Canis) species, sympatric canidae differed in body size by a factor of two or more, and differed on one or more of the parameters measuring cranial and dental shape. Such morphological differences or character displacements often have been used to infer

differences in diet, foraging strategy, or life history patterns, with the degree of such differences potentially reflecting levels of competition and/or resource stability (e.g., Cody 1974, Ricklefs et al. 1981, Van Valkenburgh 1985, Dayan et al. 1989).

Interspecific relationships between sympatric canids are basic factors in formulating management strategies. The success of efforts to conserve a threatened or endangered canid species or to mitigate the effect of a "pest" species may depend upon the interactive role of other sympatric canid species. The potential for hybridization between canid species causes added complications for conservation efforts (O'Brien and Mayr 1991, Geist 1992).

In this paper we review the interactions and ecological relationships of sympatric canids and discuss the ecological factors promoting this sympatry. Specifically we compare ecological parameters considered important in assessing potential resource competition including body mass, social system, and degrees of prey, spatial, habitat, and temporal overlap. We also explore how competition may alter behavioral and ecological patterns, discuss the role of sympatry in the conservation and management of canid species, and identify areas of future research.

METHODS

The Latin and English names used for this review are summarized in Table 1. We used the nomenclature and geographic regions used by Ginsberg and Macdonald (1990), except that South American canids are referred to as foxes instead of zorros. Within each geographic region, potential areas of current and historical sympatry were identified on the basis of distribution and broad habitat utilization records.

Six assemblages of coexisting canidae are examined in depth: black-backed jackal (Canis mesomelas), golden jackal (C. aureus), side-striped jackal (C. adustus), African wild dog (Lycaon pictus), and bat-eared fox (Otocyon megalotis) in east Africa; culpeo fox (Dusicyon culpaeus) and South American grey fox (D. griseus) in southern South America; grey wolf (C. lupus), coyote (C. latrans), and red fox (V. vulpes) in the northern United States and southern Canada; red fox and arctic fox (Alopex lagopus) in northwestern Canada and Alaska; coyote, red fox, and grey fox (Urocyon cinereoargenteus) in the southeastern United States; and dingo (C. familiaris dingo) and red fox in Australia.

We emphasize studies of clearly sympatric populations, conducted at the same time and place, to avoid results that may have been confounded by variations in food or habitat availability. When appropriate, data from single-species

studies are considered for discussion purposes. When possible, for each set of sympatric canidae, the amount of diet, spatial, habitat, and temporal overlap between each species was determined from published studies and was categorized as low, medium, or high. Variation in body mass of each species (from Ginsberg and Macdonald 1990) reflects ranges from throughout each species' distribution and not necessarily from where the species are sympatric. The predominant social system of each species in the area of sympatry was classified following Bekoff et al. (1981) as 1) solitary; 2) pairs; 3) solitary, pairs, or small groups; 4) small groups; and 5) large groups or packs.

A difficulty with this type of analysis is the variety of sampling procedures used. Conclusions of many studies were difficult to interpret because the authors failed to determine whether observed differences in resource utilization resulted from spatial segregation and differential availability of resources or if the differences reflected true mechanisms for partitioning resources.

RESULTS AND DISCUSSION

There are 34-37 canid species worldwide, depending upon the classification system used (see Wozencraft 1989). Africa and South America each support 10 species and are the two continents with the highest canid diversity. Many canids have large geographic ranges and overlap in distribution with several canid species in different areas (Table 1). Red fox is sympatric with 14 canid species, golden jackal is sympatric with 13 species and grey wolf is sympatric with 11 species. At any one location, however, the diversity of canid species is usually limited, ranging from one species to a high of five in east Africa.

Relatively few studies have examined relationships between sympatric canids, and these studies were concentrated in North America and Africa (Table 1). We found 40 studies that examined some ecological aspect of two sympatric canids, seven studies of three sympatric canids, but we found no studies that concurrently examined relationships of four or five sympatric canids. There are large gaps in our knowledge of canidae, even about many of the more common, widely distributed species.

Black-backed jackal, golden jackal, side-striped jackal, African wild dog, and bat-eared fox

These five species are sympatric in the Serengeti Plain of

Tanzania and Rift Valley of Kenya, but have never been studied concurrently. This is the largest group of sympatric canid species in the world, probably reflecting the high diversity and abundance of food in the region (Van Valkenburgh 1985). It is unclear how the five species are distributed, but African wild dog and bat-eared fox could simultaneously overlap spatially with each other and at least one of the three jackal species. Bat-eared fox, the smallest of the five species, differs ecologically from the other canids in the region by preying principally on a wide variety of insect taxa, especially termites (Hodotermes; Lamprecht 1978, Malcolm 1986, Nel 1990, Nel and Mackie 1990). African wild dog, the largest of the five species, differs from the other canids of the region by living in packs of related adult males and by preying on large herbivores such as Thompson's gazelle (Gazella thomsoni) and wildebeest (Connochaetes taurinus) in the Serengeti (Schaller 1972, Frame 1986).

Of the five species, the mechanisms of resource partitioning among the three jackals are the most uncertain. Although these three species diverged from one another more than two million years ago, they are very similar both behaviorally and morphologically (Wayne et al. 1989). Jackals of each species weigh between 7-15 kg, are omnivorous, and have a social system centered around a mated pair (Lamprecht 1978, Moehlman 1983, 1986, Fuller et al. 1989). Although

there are no obvious behavioral or physiological traits that determine jackal distribution, when sympatric they seem to segregate spatially, with side-striped jackal being found in areas of more dense undergrowth, black-backed jackal being found in woodland areas, and golden jackal being found in open plains (Fuller et al. 1989).

Side-striped, black-backed, and golden jackal, along with Cape fox (V. chama), also are sympatric in Namibia, Botswana, and the Republic of South Africa. The only concurrent ecological information on these species, however, is from incidental observations on black-backed jackal, bat-eared fox, and Cape fox by Bothma et al. (1984) in the Namib Desert, Namibia, and by Nel (1984) in the southwestern Kalahari. Bothma et al. (1984) concluded that these three species showed food-niche and temporal separation, but not spatial separation. The results of Bothma et al. (1984) are difficult to interpret because the food-habit data are from different years and the conclusions on temporal and spatial separation stem from visual sightings and not from telemetry data.

Culpeo and South American grey fox

Culpeo and grey fox are sympatric in southern South America, especially at the interface between the Andes and lowlands to the east and west. Size differences between culpeo and grey fox increase with latitude, with culpeo fox weighing 7-12 kg

and grey fox weighing 3-4 kg toward the southern portion of their ranges. Fuentes and Jaksic (1979) attributed this phenomenon to increasing sympatry between the two species, resulting in different body sizes to more efficiently partition food resources. However, Fuentes and Jaksic did not find a correlation between size differences between the two species and variations in mean size of potential prey species at different latitudes; prey size remained constant.

The most detailed study of the two species when sympatric was conducted in Torres del Paine National Park in the Patagonia of southern Chile (see Sections 2-3). Culpeo fox had significantly more remains of European hare (Lepus capensis) and fewer remains from carrion in its feces and grey fox fed more on insects and berries. The two species also occupied different habitats, with grey fox being found in more open, upland grassland and shrub transition habitats, whereas culpeo fox used more dense, matorral shrubland or Nothofagus thicket. We concluded that observed differences in prey habits and habitat utilization could be attributed to differences in resource availability in the nonoverlapping home ranges of culpeo and grey fox, as both fed on the same food items and selected for the same habitat types within their home ranges. Differential energy needs related to body mass, led us to hypothesize that the ranges of both species were determined by the more dominant culpeo fox, which

occurred where densities of medium-sized prey species were sufficient (see Section 4).

Grey wolf, coyote, and red fox

These three species are currently sympatric throughout much of the northern United States and southern Canada and have been the most intensely studied of the groups of sympatric carnivores. Yet, researchers remain uncertain what factors influence the distribution of the three species, and it is unknown whether they compete or what limiting resources might be factors in such competition. As is true of other sympatric canids, the distribution of these three species has changed dramatically during the last 200 years. The present distribution of wolves, coyotes, and red fox is influenced strongly by altered habitats, altered prey availability, and the altered competitive structure within the community. Red fox has expanded its range south and west from its original distribution in the northern parts of the continent. Coyote, previously confined to mainly arid areas in western North America, is currently found in every state, province, and country north of Panama. Grey wolf, once distributed across most of North America, has been extirpated south of the 48th parallel (Schmidt 1986).

Numerous authors have attributed these changes in distribution to habitat alterations by humans, which have

generally favored red fox and coyote and not grey wolf, and to a strong negative interaction between the three canids. There is substantial evidence of an inverse relationship between the population densities of grey wolf and coyote (Berg and Chesness 1978, Carbyn 1982) and coyote and red fox (Robinson 1961, Linhart and Robinson 1972, Sargeant 1982, Cowardin et al. 1983). One of the proximate causes of this numerical response may be the exclusion or displacement of coyote by grey wolf (Berg and Chesness 1978, Fuller and Keith 1981) and of red fox by coyote (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989, Ingle 1990) through active aggression by the larger canid and/or avoidance by the smaller one (Fuller and Keith 1981, Carbyn 1982, Dekker 1983, 1989, Sargeant and Allen 1989).

Alternatively, the apparent spatial segregation could result from differential preferences in habitat or prey selection (Todd et al. 1985), especially between coyote and red fox, whose home ranges do not seem to overlap as readily as those of grey wolf and coyote (Sargeant and Allen 1989, Paquet 1991). In support of this contention, some studies have found that coyote and red fox select different habitats within the same area (Major and Sherburne 1987, Theberge and Wedeles 1989). Also, although coyote and red fox generally feed on the same food items, they do so in different proportions (Green and Flinders 1981, Chambers 1987, Major and

Sherburne 1987, Theberge and Wedeles 1989, Dibello et al. 1990).

Using a slightly different argument, Paquet (1992) proposed that the association of grey wolf and coyote was influenced largely by prey availability. He hypothesized that grey wolf distribution was determined by the availability of large ungulate prey species and that coyote was excluded from or avoided these areas unless it was able to scavenge on carrion from the kills of grey wolf. Paquet (1992) and Meleshko (1986) suggested that food-resource partitioning, with the larger grey wolf preying on larger prey species, also facilitated the spatial overlap of these two canids. Similarly, Schmitz and Lavigne (1987) concluded that differences in the sizes of grey wolf and coyote could be accounted for by differences in their food habits, and not evolutionary pressures between these two competing carnivores.

Only brief observations have been made on the relationship between grey wolf and red fox (Andriashek et al. 1985, Dekker 1989), but Mech (1970) concluded that red fox probably benefitted by association with grey wolf because of the food provided by carrion and abandoned kills. Little is known about the interactions between kit fox (Vulpes macrotis) and other canids, but coyotes are known to kill kit fox (Scott-Brown et al. 1987).

Red fox and arctic fox

These two species are sympatric in Alaska and northwest Canada. Smits et al. (1989), in the only concurrent study on sympatric populations of red fox and arctic fox, determined that the two species have similar summer food habits, leading to potential competition. Similarly, Hersteinsson and Macdonald (1982), on the basis of similarities in morphology, social organization, and resource utilization, determined that the two species would be direct competitors where sympatric.

Arctic fox was subordinate to red fox in an artificial enclosure (Rudzinski et al. 1982) and appeared to avoid close encounters with red fox in the wild (Schamel and Tracy 1986). In spite of this apparent behavioral dominance, red fox has not been observed excluding arctic fox from any area where they were sympatric. The ability of red fox to outcompete and exclude arctic fox from an area may, however, be attenuated by the greater capacity of arctic fox to withstand colder temperatures and ability to acquire winter food (Chesemore 1975, Smits et al. 1989).

Coyote, red fox, and grey fox

These three species are sympatric in portions of southeastern United States. Although these species are economically and ecologically important furbearers, there is no general agreement on their relationships to one another and relatively

few empirical studies have been done on sympatric populations, especially including grey fox. These canids have become more sympatric in the last 300 years as the coyote has expanded its range eastward and as red fox was introduced and became established in eastern North America in the 17th century (Mansueti 1955).

There have been conflicting opinions, based largely on circumstantial evidence, on whether or not there is an inverse relationship in population density in coyote and grey fox (Davis 1966, Small 1971, Stoudt 1971, Sargeant 1982, Wooding 1984) and red and grey fox (Trapp and Hallberg 1975).

Several studies have found overlap in red and grey fox home ranges (Follman 1973, Schloeder 1988, Sunquist 1989, Ingle 1990) with varying degrees of differential habitat use. Grey fox have generally been found to use the more wooded areas and red fox to use the more open habitats. As discussed previously, home range overlap between red fox and coyote seems to be rare. In contrast, overlap of grey fox home ranges with coyotes seems to be more common, with grey foxes using slightly different habitats (Wooding 1984) than coyotes do or grey fox avoiding coyote activity centers both temporally and spatially (Ingle 1990). Unfortunately, none of these studies included an adequate analysis of the food habits of these sympatric canids.

Concurrent food habit studies of these three carnivores

are rare. King (1981) found that coyote, red fox, and grey fox fed on the same food types in winter in northeast Arkansas, but in different proportions. In an apparent contradiction King concluded that although diet overlap was high among the three species, that their diets were only superficially similar and would not result in significant competition. Hockman and Chapman (1983) analized stomachs collected during two years in Maryland and also found a large amount of diet overlap. They concluded that the probability of competition is reduced because red fox feeds primarily on small mammals and that grey fox is more omnivorous. Using a different approach, Jaslow (1987) concluded that morphological and physiological differences between red and grey fox may facilitate sympatry by allowing each species to exploit different foods more effectively.

Dingo and red fox

These two non-native species have been sympatric in Australia since the early 1900s, when red fox was introduced into Australia, joining the dingo, which was introduced about half a century earlier (Long 1987). Feeding habits of these two canids have been extensively studied separately, but not concurrently in the same time and place. Brown (1990) found that dingo feed on large- and medium-sized prey whereas red fox fed on medium- and small-sized prey species. Marsack and

Campbell (1990) documented several occasions of dingo preying on red fox.

Generalizations from sympatric studies

It is obvious that canid species can successfully coexist in sympatry. The number of sympatric canids in a given area seems to be determined by a combination of biogeographical history, human intervention, and environmental diversity and productivity. For example, a large number of sympatric canids occur in portions of eastern and southern Africa because of the heterogeneous environments and large diverse populations of ungulates. Canids, which are coursing predators, are especially well adapted to these open terrains. In contrast, Australia, because of its unique biogeographical isolation, has only two introduced species, dingo and red fox, both of which are thriving in spite of human persecution.

Several patterns emerge when we examine the trends in how 13 different pairs of sympatric canid species partition resources (Table 2). Temporal partitioning of resources does not seem very common in canids; all 13 pairs that we compared showed a medium to high amount of overlap in periods of activity. But, none of the pairs of sympatric canids demonstrated a high degree of both spatial and diet overlap. Of the pairs from which there is sufficient information on both spatial and diet overlap, three pairs seem to segregate

themselves in different areas, and one pair uses different food resources. Spatial overlap combined with differential habitat use seems to be a less common means of resource partitioning.

This pattern suggests that, at least in those cases where food habits are similar, competition for food resources may help determine spatial distributions of sympatric canids. In these cases, the mechanisms of suppression or displacement are still unproven, but are likely to involve a combination of exclusion by the dominant species and avoidance by the subordinate, depending upon the ecological circumstances. Predation of one canid on another does not seem to be common, although aggression, from nonphysical to lethal, has been well documented between several canid species, most notably between grey wolf and coyote, coyote and red fox, and dingo and red fox.

Conservation Implications

There are several ways that the interactions between sympatric canid species can have a strong influence on canid conservation and management efforts. Changes in canid community structure usually follow the range expansion, extirpation, or reintroduction of a canid species. The best-documented case is that of coyote, which may have been able to expand its range, in part, because of the elimination of grey

wolf. The coyote has also rapidly expanded its range south into Central America, after changes in habitat associated with increased human development and agricultural clearing of primary forest (Vaughan 1983). This could affect South American canid communities, especially if coyote were successful in naturally or artificially crossing the barrier of the humid tropics of Panama into South America.

Red fox, which also may have benefitted from the removal of grey wolf in parts of its range, and which is expanding its distribution worldwide, could have a similar effect on local canidae. Hersteinsson et al. (1989) believe that the red fox, which has become more common as grey wolf have been eradicated, may represent the greatest threat to arctic fox in Scandinavia. Similarly, Hersteinsson and Macdonald (cited in Ginsberg and Macdonald 1990) believe that range expansion of red fox may be the most critical threat to the long-term survival of many of the lesser known small canid species of North Africa and the Middle East.

Interspecific relationships among canids will also have to be considered before the implementation of canid reintroduction programs, which will probably become increasingly important to canid conservation. Because most reintroduction efforts will attempt to restore past community structure, interspecific relationhips will be of most concern when existing canidae, either directly or indirectly, reduce

the probability of successful reintroduction. For example the reintroduction of red wolf into parts of southeastern United States may eventually be jeopardized by the potential hybridization of newly released wolves or their offspring with resident coyotes, as has happened in other areas (Schmitz and Kolenosky 1985, Lehman et al. 1991, Wayne and Jenks 1991). In other instances, such as the possible reintroduction of grey wolf into parts of western United States, the concern will be with the effect on resident coyote and red fox populations and the resulting changes that could occur with the prey community (Bob Crabtree, pers. commun.).

Needed Research

In spite of the evidence supporting the prevailing idea that sympatric canids compete for available resources, it remains unproven that canid communities or assemblages are structured by interspecific relations. In addition to the descriptive studies which have been most common, more detailed and carefully planned studies are needed on sympatric canids. There are several approaches which may be particularly useful in resolving the issues concerning sympatric canidae.

At the very least, studies of sympatric canids need to address how species are selecting and utilizing resources within their individual home ranges, instead of the whole study area. Perceptions of habitat and food preferences might

change dramatically with a more detailed and accurate accounting of resource availability for each individual. This is especially important when there is no spatial overlap of home ranges between species or when there is considerable variability among individuals. Ideally this information should be combined with data on resource utilization of the species when populations are not sympatric. This could be accomplished through studies at different places or times that had different canid assemblages, or it could be done through the experimental removal or introduction of one species.

Other experimental studies which would be of value include greatly increasing, decreasing, and/or changing food availability to see if community structure changes. A sufficient amount of large-prey items may be important for maintaining the populations of larger canids such as wolf or culpeo fox, which, in turn, may modify the distributions of smaller canids such as coyote or South American grey fox respectively. Monitoring the effects of canid reintroduction programs such as may occur with wolves in western United States also would provide opportunities for natural experiments.

Canids are wide ranging and often difficult to observe and catch, and there are several family characteristics that make these experimental studies challenging. Because most canids are generalists and are adaptable to a wide variety of

environmental conditions, their responses to natural changes or human perturbations may initially not be obvious. Also, because canids are highly mobile and have flexible socioecologies, idividuals within a species are likely to respond differently to experimental manipulation. Finally, recent and continuing changes in canid distribution imply that, in some cases, results of competitive interactions may not yet be apparent and may still be evolving.

ACKNOWLEDGMENTS

We thank Lou Best, William Clark, and Irv Klass for their valuable comments on the manuscript. This study was made possible by grants from the National Geographic Society, Patagonia Research Expeditions (Iowa State University), the Organization of American States, the International Telephone and Telegraph Corporation Fellowship Program, and the National Wildlife Federation. Journal Paper No. J-14873 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2519.

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Table 1. Sympatry between canid species in five regions of the world. P = Predicted sympatry based on geographic distributions; S = Sympatry confirmed in field studies; H = Historical but not current sympatry.

Sub-Saharan Africa[a]

	C. adu	C. aur	C. mes	C. sim	L. pic	O. meg	V. cha
Canis adustus Side-striped jackal	-	S	S		P	P	
C. aureus Golden jackal		-	S		P	P	
C. mesomelas Black-backed jackal			-		P	S	S
C. simensis Simien jackal				-			
L. pictus African wild dog					-	P	
O. megalotis Bat-eared fox						-	S
V. chama Cape fox							-

South America[b]

	C. tho	C. bra	D. cul	D. gri	D. gym	D. mic	D. sec	D. vet	S. ven	U. cin
Cerdocyon thous Crab-eating zorro	-	P			P	P		P	P	P
Chrysocyon brachyurus Maned wolf		-			P			P		
Dusicyon culpaeus Culpeo zorro			-	S	P		P			
D. griseus Grey zorro				-	P					
D. gymnocercus Azara's zorro					-					
D. microtis Small-eared zorro						-			P	
D. sechurae Sechuran zorro							-			
D. vetulus Hoary zorro								-		
Speothos venaticus Bush dog									-	P
Urocyon cinereoargenteus Grey fox										-

Table 1. (continued)

Holarctic[c]

	A. lag	C. lat	C. lup	C. ruf	N. pro	U. cin	U. lit	V. vel	V. vul
A. lagopus Arctic fox	-	S	S						S
C. latrans Coyote		-	S			S		S	S
C. lupus Gray wolf			-		S			H	S
C. rufus Red wolf				-		H			
N. procyonoides Raccoon dog					-				S
U. cinereoargenteus Gray fox						-		S	S
U. littoralis Island gray fox							-		
V. velox Swift or kit fox								-	
V. vulpes Red fox									-

North Africa and the Middle East[d]

	C. aur	C. lup	F. zer	V. can	V. pal	V. rue	V. vul
C. aureus Golden jackal	-	P	P	P	P	P	P
C. lupus Grey wolf		-		P		P	
F. zerda Fennec fox			-				P
V. cana Blanford's fox				-		P	P
V. pallida Pale fox					-		
V. rueppelli Ruppell's fox						-	S
V. vulpes Red fox							-

South and Southeast Asia and Australia[e]

	C. aur	C. fam	C. lup	C. alp	V. cor	V. ben	V. fer	V. vul
C. aureus Golden jackal	-		P	P	P	P		P
C. familiaris dingo Dingo		-		P				P
C. lupus Grey wolf			-	P	P	P	P	P
C. alpinus Dhole				-	P	P		P
V. corsac Corsac fox					-			P
V. bengalensis Bengal fox						-		P
V. ferrilata Tibetan fox							-	P
V. vulpes Red fox								-

a. C. mesomelas, O. megalotis, and V. chama: Bothma et al. (1984), Nel (1984); C. adustus, C. aureus, and C. mesomelas: Fuller et al. (1989); C. aureus, and C. mesomelas: Lamprecht (1978), Moehlman (1983); C. aureus, C. mesomelas, and L. pictus: Schaller (1972)

b. D. culpaeus and D. griseus: Fuentes and Jaksic (1979), Jaksic et al. (1983)

c. C. lupus, C. latrans, V. vulpes: Dekker (1989); C. latrans, V. vulpes: Robinson (1961), Linhart and Robinson (1972), Johnson and Sargeant (1977), Green and Flinders (1981), Sargeant (1982), Dekker (1983), Voigt and Earle (1983), Engelhardt (1986), Schmidt (1986), Chambers (1987), Klett (1987), Major and Sherburne (1987), Sargeant et al. (1987), Harrison et al. (1989), Sargeant and Allen (1989), Theberge and Wedeles (1989); C. lupus, C. latrans: Berg and Chesness (1978), Fuller and Keith (1981), Carbyn (1982), Cowardin et al. (1983), Schmitz and Lavigne (1987), Paquet (1991), Paquet (1992); C. latrans, U. Cinereoargenteus: Wooding (1984); V. vulpes, U. Cinereoargenteus: Wood et al. (1958), Follman (1973), Ashby (1974), Yearsley and Samuel (1980), Hockman and Chapman (1983), Schloeder (1988), Sunquist (1989); C. latrans, V. vulpes, U. Cinereoargenteus: King (1981), Ingle (1990); V. vulpes, A. lagopus: Smits et al. (1989)

d. V. rueppelli and V. vulpes: Lindsay and Macdonald (1986)

e. C. familiaris dingo and V. vulpes: Brown (1990), Marsack and Campbell (1990)

Table 2. Summary of interspecific relationships between pairs of sympatric canids.

Species	Body mass (kg)	Prey overlap	Spatial overlap	Habitat overlap	Temporal overlap	Aggression documented	Social system similar
C. lupus C. latrans	16-60 9-16	low-medium	low-high	-	high	yes	no
C. latrans V. vulpes	9-16 3-11	medium-high	low	low-medium	high	yes	yes
C. cinereoargenteus C. latrans	3-7 9-16	-	high	medium	high	no	yes
V. vulpes A. lagopus	3-11 3-4	high	-	-	-	yes	yes
C. cinereoargenteus V. vulpes	3-7 3-11	-	medium	high	-	no	yes
D. culpaeus D. griseus	8-12 3-4	medium	low	medium	high	no	yes
C. mesomelas O. megalotis	9 4	low	-	-	medium	no	yes
C. mesomelas V. chama	9 3	low	-	-	medium	no	yes
O. megalotis V. chama	4 3	low	low	-	medium	no	yes
C. aureus C. mesomelas	7-15 6-12	high	low	low	medium	yes	yes
C. aureus C. adustus	7-15 6-14	-	-	low	medium	no	yes
C. mesomelas C. adustus	6-12 6-14	-	-	low	medium	no	yes
C. familiaris dingo V. vulpes	9-22 3-11	low	-	-	-	yes	yes

SECTION 2.

PREY SELECTION BY GREY AND CULPEO FOX (*DUSICYON GRISEUS* AND *D. CULPAEUS*) IN THE PATAGONIA OF SOUTHERN CHILE

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PREY SELECTION BY SYMPATRIC GREY AND CULPEO FOX (*DUSICYON GRISEUS* AND *D. CULPAEUS*) IN THE PATAGONIA OF SOUTHERN CHILE

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ABSTRACT.--The feeding ecology of sympatric South American grey fox (*Dusicyon griseus*) and culpeo fox (*D. culpaeus*) was studied from 1987 to 1990 in the eastern part of Torres del Paine National Park, Chile, to determine if, as predicted, they have different patterns of prey selection. Seasonal and species differences in prey selection were compared with prey availability to determine if they reflected a selection by the fox species. Mammals accounted for 90% of the 851 vertebrate prey items found in 890 grey fox feces. European hare (*Lepus capensis*) was the most common vertebrate found in

the feces (45%), with lesser amounts of guanaco (Lama guanicoe, 14%) and Akodon species (13%). Of 784 vertebrate prey items found in 645 culpeo feces, 93% were from mammals. European hare accounted for 69% of the prey items and rodent species 20%. The proportion of vertebrate prey items consumed by grey and culpeo fox changed seasonally. Grey and culpeo fox yearly diets were significantly different, with ungulates and European hare contributing most to the difference. Grey fox were more omnivorous than culpeo fox, feeding more on beetles and plants, especially from spring through fall. Grey fox had a significantly higher index of standardized vertebrate food-niche breadth than culpeo fox (0.24 ± 0.01 versus 0.09 ± 0.01; mean ± SE) and had a significantly lower mean vertebrate prey mass (2.17 ± 0.07 versus 2.59 ± 0.09 kg). The index of similarity or overlap between fox diets was low (0.14). Differences in feeding habits between grey and culpeo fox are evidently attributable to differences in food availability in their respective habitats.

INTRODUCTION

Culpeo (Dusicyon culpaeus) and South American grey fox (D. griseus) are found east and west of the Andes from northern Chile and Argentina south to the island of Tierra del Fuego (Osgood, 1943; Crespo, 1975; Ginsberg and Macdonald, 1990). The most detailed knowledge of these foxes is on their food habits (Medel and Jaksic, 1988), although small sample sizes and disparate sampling methods reduce the reliability of generalizations based on these data. Throughout their range, the two fox species depend heavily on rodents (mice), but they also feed locally and seasonally on lagomorphs (rabbits and hares), lizards, birds, carrion, insects, and plant matter such as berries (Jaksic et al., 1980; Jaksic et al., 1983; Simonetti et al., 1984). These studies suggest that both species display opportunism and trophic plasticity.

Although both species have been well studied in comparison with other South American canids (reviewed by Medel and Jaksic, 1988; Ginsberg and MacDonald, 1990), detailed concurrent studies on both species have not been done. Grey and culpeo fox diverged only 250,000 years ago (Wayne and O'Brien, 1987; Wayne et al., 1989) and ecological theory predicts that for these two closely related carnivores to coexist they will reduce interspecific competition by partitioning resources (Rosenzweig, 1966).

One of the principle mechanisms for reducing competition

in vertebrates is different food habits. Because body size is often correlated with prey size (Rosenzweig, 1968), dissimilar body sizes are frequently cited as an indication of food resource partitioning. Thus, the degree of competition between two species may be dependent on differences in body size (Pacala and Roughgarden, 1985; Moulton and Pimm, 1986).

Size differences between grey and culpeo fox increase with latitude, with culpeo fox weighing 7-12 kg and grey fox 3-4 kg toward the southern portion of their range. Fuentes and Jaksic (1979) attributed this phenomenon to increasing sympatry between the two species and the need to partition food resources. However, they did not find the predicted correlation between size differences in the two species and variations in mean size of potential prey species at different latitudes; prey size remained constant. Fuentes and Jaksic (1979) also did not compare actual prey sizes which may have better explained differences in body size (McNab, 1971).

Diets of sympatric grey and culpeo fox from continental and insular (Tierra del Fuego Island) populations of southern Chile were compared by Jaksic et al. (1983). They did not find any differences in mean weight of vertebrate prey between grey and culpeo fox, but they concluded that since the similarity in diet between island populations of grey and culpeo foxes was less than between mainland populations in central Chile, that sympatric populations showed greater

dietary divergence. These conclusions are weak, however, because they were made on the basis of a small number of feces and stomachs (n = 7, 9, 95, and 116) collected in different areas during different years.

The primary objective of our study was to compare the feeding ecology of sympatric grey and culpeo fox and to determine if, as predicted, they have different patterns of prey selection. We also address whether seasonal and species differences in prey selection are related to prey availability or if they reflect selection by the fox species.

STUDY AREA

This study was conducted from 1987 to 1990 in 21,000 ha of the eastern part of Torres del Paine National Park (51°3'S, 72° 55'W), located in the eastern foothills of the Andean mountain range in southern Chile. The Park encompasses 2,400 km^2 and provides almost undisturbed habitat for wildlife.

Plant associations and habitats within the Park are heterogeneous, ranging from glacier-covered mountains to dense Nothofagus deciduous forest and grassland. Approximately 70% consists of a steppe biome, or pre-Andean, dry shrub association, and the remainder is a mosaic of lakes, forests, and arid-mountain alpine zones. The steppe is characteristic of the southern South America pampa found in Chile and Argentina at elevations below 500 m (Pisano, 1973, 1974). We estimated prey availability in six habitat types: 1) exposed rocks and unvegetated soil, 2) upland grassland, 3) upland shrub transition (grass and shrubs < 1 m high), 4) mata negra transition (mata negra and shrubs < 1 m), 5) matorral shrubland, and 6) Nothofagus thicket. Upland grassland includes the vega (wet meadow), coirón (bunch grass), and hierba (forb) communities described by Ortega & Franklin (1988). Dominant grass species of this habitat are Festuca gracillina, Anarthrophyllum patagonicum, and F. palliscens, in order of decreasing cover (Pisano 1973, 1974; Texera 1973;

Ortega & Franklin 1988). Upland shrub transition habitat is a continuum from grassland to dense, continuous stands of low shrubs < 1 m high. The locally dominant shrub species is "mata barrosa" (Mulinum spinosum) and other common shrub species are "senecio" (Senecio patagonicus), "calafate" (Berberis buxifolia), and "paramela" (Adesmia boronoides). Mata negra transition habitat is also a continuum from grassland to bushes, but is dominated by "mata negra" (Verbena tridens). Matorral shrubland is a varied, more dense habitat, often containing many of the species common in upland shrub transition and mata negra transition habitats, but also including low woody vegetation averaging around 1.5 m tall. Characteristic trees or tall shrubs of this habitat are Nothofagus pumilio, Escallonietum rubrum, and Embothrium coccineum. Plant species of Nothofagus thicket habitat are often the same as those in matorral shrubland, but they are found in larger stands of taller trees rarely > 10 m, with a more open understory.

The Park has a high diversity of mammalian species (Johnson et al., 1990). Potential mammalian prey species included guanaco (Lama guanicoe), introduced European hare (Lepus capensis), domestic sheep (Ovis aries), and several cricetine rodents such as Auliscomys micropus, Oryzomys longicaudatus, Phyllotis darwini, Reithrodon physodes, and five Akodon species. Numerous avian species were also

potential prey items for foxes, including upland goose (Chloephaga picta). The puma (Felis concolor), Geoffroy's cat (F. geoffroyi), Patagonia hog-nosed skunk (Conepatus humboldtii), Patagonia weasel (Lyncodon patagonicus), and several raptors (Iriarte et al., 1990), including great horned owls (Bubo virginianus) and black-chested buzzard-eagle (Geranoaetus melanoleucus), were potential competitors.

We separated the data into four, 3-month climatic periods, or seasons, based on temperature, precipitation, wind, and biological activity of the park's wildlife. Summer (December - February) is windy, rainy, and relatively warm (January mean daily temperature is 12.6°C) (temperatures from records obtained from 1985 to 1987 at park headquarters). Winter (June - August) is dry, less windy, and relatively cold (mean daily July temperature is 0.2°C). Spring and Fall are intermediate in temperature and have less predictable wind patterns.

Mean annual precipitation is 550 mm, with 60% falling from January to May. Adjacent mountains and ice fields create local weather patterns, reflected by a large variability in precipitation (Pisano, 1974).

METHODS

Prey utilization.--Food habits were determined from analyses of feces collected from March 1987 through June 1989 from throughout the study area. Estimated age, location, and date were recorded for each fecal sample; time since deposition was estimated by comparison with feces of known age. We were confident that collected feces were from canid species because the only potential misidentifications were feces from Geoffroy's cats, which generally defecated in middens and in trees (Johnson and Franklin, 1991), and puma feces, which were noticeably more log-shaped, less twisted, and much larger. Feces along roads or other areas commonly used by domestic dogs were not collected, although domestic dog feces were usually distinguishable because they had few remains of bone, hair, and beetles. Because there was little interspecific overlap in fox home ranges, as determined by radio-telemetry techniques (see Section 3), grey and culpeo fox feces were distinguished by their location in association with distributions of marked individuals. Frequent sightings of grey and culpeo fox, due to their habituation to observers, increased the reliability of the distributions determined for each species. Feces that could not be confidently attributed to a species, either from its location or shape, were not included in analyses.

Feces were air-dried and the major components were

separated. Hard parts (bones, teeth, toe-nails, hair, and feathers) were identified to species for mammals and to family for birds by direct comparison to reference specimens or by using keys from Reise (1973) and Pearson (1986). Results were presented as percent occurrence (number of times a prey item was found as percentage of the total number of prey items found in all scats) for vertebrate prey items. Presence of invertebrate prey items, such as beetles, and plant remains was expressed as percentage of feces that contained remains of that item. Food habit analysis was divided into each of the four seasons.

Seasonal and interspecific differences in percent occurrence of vertebrate prey items in feces were tested by Chi-square analysis (PROC FREQ, SAS Inst., 1989). Because there was not any significant association between years and occurrence of prey items in feces of either species (grey fox: $\underline{X}^2 = 4.04$, 4 df, $P = 0.40$; culpeo fox: $\underline{X}^2 = 1.87$, 4 df, $P = 0.75$), data from feces collected during different years were combined for analysis. Prey items were categorized as rodents, hares, birds, ungulates, or other for Chi-square tests. Once a significant relation was established, individual Chi-square values of each prey category were compared with Bonferroni normal statistics to examine the item's influence (Neu et al., 1974; Johnson and Wichern,

1982:197). Differences were considered significant when individual Chi-square scores had an alpha level less than 0.05 / number of categories.

Mean mass of vertebrate prey was calculated as in Iriarte et al. (1991) by using only prey items identified to species (with the exception of Akodon spp., which were analyzed together) and excluding guanaco (Lama guanicoe), cattle, and sheep, which were considered to be scavenged. Although culpeo fox are capable of preying on sheep (Crespo and de Carlo, 1963; Bellati, 1985), there was no evidence that they were a significant cause of sheep mortality. Average body masses of prey species were determined from juveniles and adults captured throughout the year and from estimates made by Johnson et al. (1990).

Colwell and Futuyma's (1971) standardized form (B_{sta}) of Levins' index (B) was used to measure vertebrate food-niche breadth (Levins 1968), an index of diet diversity. $B_{sta} = (B_{obs} - B_{min}) / (B_{max} - B_{min})$ where B_{obs} is the observed niche breadth, B_{min} is the minimum niche breadth and B_{max} is the maximum possible niche breadth (the number of taxa taken). $B_{obs} = 1 / p_i^2$ where p_i is the relative occurrence (proportion) of prey taxon i in the diet. Food-niche breadth was measured for each fox species at the highest level of taxonomic resolution of prey categories. Standardized food-niche breadth makes it possible to compare

diets with different numbers of prey categories; the scale of the index ranges from zero to one, or from narrow to broad food-niche breadth. Standardized food-niche breadth was not correlated with sample size ($r = 0.07$, $F = 0.03$, 1 df, $P = 0.86$). Significant differences ($P < 0.05$) in mean mass of vertebrate prey and standardized food-niche breadth between the two fox species were tested by averaging across seasons and using t-tests. Food-niche overlap, a measure of dietary similarity, was calculated by using Pianka's (1973) index, where $o = \Sigma\ p_{ij}\ p^{ik} / (\Sigma\ p_{ij}^2\ \ \Sigma\ p_{ik}^2)^{½}$. This index ranges from 0 to 1, or from complete dissimilarity to similarity.

Prey Availability.--The availability of small rodents and beetles was compared in 5 of the 6 habitat types (excluding rock and bare ground habitat) in the study area. Small rodents were captured in Shermann live-traps placed in permanent 7 x 7 grids with 10 m between each trap. Grid location was chosen randomly within large areas of uniform habitat. Traps were baited with a mixture of rolled oats, hot water, and sheep lard, and were checked every morning. Upland grass habitat was sampled for three days each month from March 1987 to February 1988 after which sampling was discontinued because only one individual was captured during this time. Upland shrub transition, mata negra, matorral shrubland, and Nothofagus thicket habitats were sampled four days each month

from May 1988 to April 1989.

Monthly population size of small rodents and standard error estimates were obtained from Program CAPTURE (White et al., 1978) using Model M_h, which allows capture probabilities to vary by animal and has the most robust estimator (White et al., 1982). Observations in which a dead animal was found in a trap before the last day of trapping were removed from the capture history and added to the total estimate of population size after the analysis was completed. Monthly values were averaged to obtain seasonal estimates of population size and standard error. Analysis of variance was used to test for significant differences in estimated number of small rodents among seasons and habitats and the Ryan-Einot-Gabriel-Welsch multiple-range test was used to test for significant differences among main effects means (PROC GLM, SAS Inst. 1989). Only habitats with an average estimated seasonal population size > 15 and an average capture probability > 0.45 were used for these tests because obtaining unbiased and precise estimates is difficult with small sample sizes. If seasonal averages failed to meet these criteria, the total number of distinct individuals captured (N_{t+1}) each month was reported as an index of seasonal abundance and standard error, and no statistical inferences were made.

Numbers of beetles (Coleoptera) in each habitat were

measured by using 12-cm-diameter pitfall traps. Five traps, four located at the corners and one at the center of the small rodent trapping grids (60 x 60m), were filled with 10% formaldehyde solution and checked monthly from October, 1987, to March, 1988, the same time period as virtually all above-ground beetle movement. Beetles were identified to the species level by comparing them with a reference collection at the Patagonia Institute, Magallanes University, Punta Arenas, Chile. Analysis of variance was used to test for significant differences in number of beetles among seasons and habitats, and the Ryan-Einot-Gabriel-Welsch multiple-range test was used to test for significant differences among main effects means (PROC GLM, SAS Inst., 1989).

European hare densities were estimated monthly from July 1987 to June 1989 for the areas occupied by radio-collared grey and culpeo foxes. Data was collected by 1-2 people walking seven transects totaling 5.44 km randomly located within the grey fox distribution area, and walking three transects totaling 4.84 km randomly located in the culpeo fox distribution area. Density and standard error estimates of densities were calculated from the Fourier series estimator in Program TRANSECT (Burnham et al., 1980). Significant differences in monthly European hare estimates between fox distribution areas and among seasons were determined by using analysis of variance (PROC GLM, SAS Inst. 1989).

To summarize food selection patterns, the availability and utilization of small rodents, European hares, carrion, beetles, and fruit were classified as low, same, or high for each fox species in comparison with the other. Selectivity measures of these categories were classified subjectively as none, for, or against when there were clear patterns.

RESULTS

Mammals accounted for 90% of the 851 vertebrate prey items found in 890 grey fox feces (Table 1). European hare was the most common vertebrate prey (45%), with lesser amounts of guanaco (14%) and Akodon species (13%). The proportion of vertebrate prey items consumed by grey fox was associated with season ($\underline{X}^2 = 45.4$, 12 df, $P < 0.001$). Frogs and lizards contributed most to the difference ($\underline{X}^2 = 23.39$, $P < 0.01$). They represented from 4 to 9% of the prey items from spring to fall, but were not found during the winter. Beetles were found in the greatest proportion of feces during spring and summer (57% and 60%, respectively), and calafate seeds (8%) were more common in summer (15%) and fall (14%).

Of 784 vertebrate prey items present in 645 culpeo feces, 93% were from mammals (Table 2). European hare accounted for 69% of the prey items and rodents accounted for 20%. Vertebrate prey items in culpeo fox feces were associated with season ($\underline{X}^2 = 21.3$, 12 df, $P = 0.047$). Beetles and calafate berries were found in 2% and 1% of the feces, respectively.

Grey and culpeo fox diets were significantly different ($\underline{X}^2 = 155.2$, 4 df, $P < 0.001$). Ungulates ($\underline{X}^2 = 97.46$, $P < 0.001$) and European hare ($\underline{X}^2 = 39.32$, $P < 0.001$) contributed most to this difference. Grey fox had a significantly higher average seasonal index of standardized vertebrate food-niche breadth

than did culpeo fox (0.24 ± 0.01 versus 0.09 ± 0.01; T = 10.4, 6 df, P < 0.0001). Grey fox also had a significantly lower mean mass of vertebrate prey (2.17 kg ± 0.07 versus 2.59 kg ± 0.09; T = 3.4, 6 df, P = 0.01). Food niche overlap between diets of the two foxes was low (0.14).

Estimates of small rodent numbers were significantly different among habitats (F = 6.14, 2, 32 df, P = 0.008) and among seasons (F = 3.35, 3, 32 df, P = 0.04), but the interaction of habitat by season was not significant (F = 1.72, 6, 32 df, P = 0.17). There was not a significant difference (21 df, P > 0.05) between Nothofagus thicket and matorral shrubland habitats, which had the highest estimated numbers of small rodents, nor between matorral shrubland and mata negra habitat (Table 3). Small rodents were significantly more abundant during fall.

Mean number of beetles captured was significantly different among habitats (F = 9.89, 4, 149 df, P = 0.0001) and among months (F = 33.24, 5, 149 df, P = 0.0001), and the interaction of habitat by month was significant (F = 2.93, 20, 149 df, P = 0.0002). Beetles were significantly (120 df, P < 0.05) more abundant in October and November and were significantly more abundant in December than from January through March (Table 4). Upland shrub transition habitat had significantly more beetles than the other habitats. There were not any significant differences among the other habitats.

The most common beetles were Eriopsis magellanica (Coccinellidae), Barypus divinoids, (Carabidae), and Emalodera spp. (Tenebrionidae).

Mean densities of European hare were significantly different between grey and culpeo fox distribution areas ($F = 213.8$, 1, 43 df, $P < 0.0001$) and among seasons ($F = 6.8$, 7, 43 df, $P < 0.0001$), and the interaction of area and season was significant ($F = 4.8$, 7, 43 df, $P = 0.001$). Densities in both areas and in both years were highest in summer and lowest in winter, with a monthly average (± S.E.) of 24.8 ± 7.7 European hares/km^2 in the grey fox area, compared with 86.6 ± 30.0 hares/km^2 in the culpeo fox area (Fig. 1).

DISCUSSION

Diet Differences.--As predicted, South American grey and culpeo fox had different patterns of prey selection. Although both foxes preyed on essentially the same vertebrate prey categories, proportions of each category in the diets differed. Use of vertebrate prey differed significantly ($P < 0.001$) in the extent of predation on European hare and the amount of scavenging on ungulates. European hare remains were more common in culpeo fox feces; this finding also was reflected in culpeo's larger index of mean mass of vertebrate prey in comparison with grey fox. Scavenging on guanacos, sheep, and cattle was much more important for grey fox; these items represented 20% of the vertebrate prey remains in its feces, compared with less than 5% of these items for culpeo fox.

The presence of invertebrate food items in the diets of the two fox species also differed. Grey fox were more omnivorous, with a larger proportion of their feces having remains of beetles and plants, especially during spring through fall. This difference was reflected also in the significantly narrower index of standardized food niche breadth of culpeo fox, suggesting that grey fox was more of a generalist in its diet.

Diet Differences and Availability.--Differences in food resource utilization could have been related to availability,

in as much as grey and culpeo fox home ranges did not overlap spatially and were found in different habitats (see Section 3). For example, proportions of remains of European hare in fox feces paralleled hare densities. European hare densities were more than three times higher in the areas where culpeo fox were distributed. This could explain why hares accounted for 65% more of the vertebrate remains in culpeo fox feces than in grey fox feces.

Similarly, although grey fox seemed to scavenge more on carcasses, this probably reflected greater availability of large dead animals. Culpeo fox probably did not underutilize dead animals since they have previously been reported to feed on carrion (Jaksic et al., 1983). Because grey fox were found in areas of larger concentrations of guanaco and sheep, which often died of natural causes and puma predation (Iriarte et al., 1991), there was also more carrion available in grey fox areas. The lack of sheep in the diet of culpeo fox probably also reflects the absence of large numbers of sheep in the culpeo's home ranges, since culpeo fox prey on sheep in many parts of Chile and Argentina (Crespo and de Carlo, 1963; Bellati, 1985).

Remains of rodent species found in grey and culpeo fox feces also reflected differences in prey availability. Eligmodontia typus, a grassland rodent species and one of the least common rodents in the area (Johnson et al., 1990), made

up 2% of the vertebrate remains in grey fox feces, compared with 0.1% of the remains of culpeo fox. Oryzomys longicaudatus, Auliscomys micropus, and Phyllotis darwini, species found primarily in mata negra, matorral shrubland, and Nothofagus thicket habitat (Johnson et al., 1990) made up a greater proportion of the remains in culpeo fox feces than in the feces of grey fox.

For some prey categories, diets of grey and culpeo fox also followed seasonal changes in availability. Calafate berries were found in the highest percentage of fox feces in summer and fall, when berries became ripe. Beetles also were consumed more in spring and summer, when they were most common, and became less common in feces as insect abundance decreased during fall.

Diet Differences and Selection.--Although there were differences in food availability in habitats occupied by grey and culpeo fox, their diets did not always reflect these variations. For example, the two species responded differently to the availability of calafate berries and beetles. Culpeo fox seemed to underutilize beetles and berries. Although beetles were available in habitats used by culpeo foxes, they were found in only 2% of culpeo fox feces. Calafate berries were even less commonly found in culpeo fox feces, although these bushes were more numerous in habitats used by culpeo fox than in habitats used by grey fox. In

contrast, grey fox were often observed actively searching for insects and berries. Rodents may also have been selected for by grey fox as rodents made up similar proportions of the remains in feces of both species even though rodents were found in greater numbers in habitats used by culpeo fox.

Grey and culpeo fox food habits did not always follow seasonal fluctuations in availability. For example, European hare densities were highest in summer and lowest in winter, but fox diets did not reflect this trend. Proportions of European hares in grey fox feces were similar during all four seasons. In culpeo fox feces the proportion of European hare was highest in spring (76%) and lowest in summer (60%). In contrast, bird remains were most common in feces of both species during spring and summer when waterfowl were more abundant and vulnerable because of nesting and the rearing of young (Garay et al., 1991).

Ecological Ramifications.--As predicted by the body sizes of the two fox species, mean mass of vertebrate prey consumed by culpeo fox was significantly heavier than for grey fox. This is not proof, however, that the larger culpeo fox is adapted to larger prey species because prey availability for each fox species was different. Indeed, grey fox preyed on almost the same species as culpeo fox, differing only in the proportion of these prey species consumed. The evidence suggests that differences in feeding habits are attributable

to differences in food availability that reflect habitat characteristics of individual home ranges as much as they are attributable to food selection. If prey availability were the same, grey fox might have a diet more similar to that of culpeo fox; although one would still predict that culpeo fox, being larger, is better adapted to feeding on larger prey species. Even the lack of berries and beetles in the culpeo fox diet may be the result of densities of more profitable prey items; given certain ecological conditions, culpeo fox may rely on these items more heavily.

There are at least three explanations for the observed dietary and distribution patterns. First, grey and culpeo fox partition habitat, rather than prey resources. We discounted this hypothesis on the basis of documented changes in fox distribution patterns apparently unrelated to habitat changes (see Section 3). Second, the constraints of body size and metabolism on optimal foraging dictate different optimal diets, and the foxes distribute themselves according to the distribution of their optimal prey, whose distribution may be linked to habitat. But this mechanism alone is unlikely to account for the nonoverlapping home ranges of grey and culpeo fox, because both species are opportunistic and flexible in their food habits and because hare and rodent populations commonly fluctuate greatly. The third, and most likely, explanation is that the optimal diets of grey and culpeo fox

are fairly similar and that culpeo fox exclude grey fox from optimal prey habitat. If grey fox are either excluded from or avoid areas occupied by culpeo fox, they would effectively be relegated to areas with less medium-sized vertebrate prey, which might force them to exploit a broader array of food categories, including more fruit and beetles. This conclusion is supported by the differential metabolic needs of grey and culpeo fox as calcualted from their body masses (see Section 4). Culpeo fox, because of their higher energetic needs, may only be distributed in areas with sufficient resources to meet these higher energy demands.

Further studies, ideally ones manipulating prey availability in areas where grey and culpeo fox are sympatric, would be useful in further understanding the use of food resources by the two fox speceies and their responses to changes in food availability.

ACKNOWLEDGMENTS

We thank the Chilean National Forestry and Park Service (CONAF) for their assistance and collaboration. We give special thanks to the personnel of Torres del Paine National Park for their help, especially Park superintendent Guillermo Santana and Park guards Oscar Guineo, Francisco Barrientos, and Juan Toro. We appreciate the dedicated field work of Gabriel Arribillaga, Fredy Barrientos, Gail Blundell, Jill Bright, Steve Catir, Lloyd Christian, Kyle Harms, Judith Hoffman, Agustin Iriarte, Andy Phillips, Barry Samson, and Steve Wilson, as well as the invaluable advice of Todd Fuller. Earlier drafts were improved by comments from Michael Behl, Lou Best, William Clark, and Irv Klaas. This study was made possible by grants from the National Geographic Society (Grant No. 3581-87), Patagonia Research Expeditions (Iowa State University), the Organization of American States, the International Telephone and Telegraph Corporation Fellowship Program, and the National Wildlife Federation. This project was conducted under a research agreement (Proyecto Puma) between Iowa State University and the Chilean National Forestry and Park Service. Journal Paper No. J-14870 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2519.

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Table 1.--Seasonal percent occurrence of vertebrate prey and percentage of feces with invertebrate remains determined from South American grey fox feces collected in Torres del Paine National Park, Chile, 1985-1989.

Prey items	Sep-Nov	Dec-Feb	Mar-May	Jun-Aug	Total
Rodentia					
Akodon spp.	8.6	10.1	13.8	16.5	12.8
Auliscomys micropus	2.7	0.6	1.8	1.1	1.5
Eligmodontia typus	2.7	1.8	2.8	1.8	2.2
Euneomys chinchilloides	0	0	0.5	0	0.1
Oryzomys longicaudatus	0.5	1.2	2.8	4.0	2.4
Reithrodon physodes	2.7	1.2	2.8	1.4	2.0
Unidentified	1.6	3.5	4.1	2.5	2.9
Total Rodents	18.8	18.4	28.6	27.4	23.9
Lagomorpha					
Lepus capensis	48.7	41.7	41.3	47.4	45.0
Carnivora					
Conepatus humboldti	0	0	1.8	0	0.5
Artiodactyla					
Bos	0	0	0.5	0.4	0.2
Lama guanicoe	10.2	14.3	11.5	17.3	13.6

Table 1. (continued)

Ovis aries	5.3	13.6	5.5	3.2	6.4
Total Ungulates	15.5	27.9	17.5	20.9	20.2
Total Mammals	83.0	88.0	89.2	95.7	89.6
Birds					
Chloephaga picta	2.1	3.0	1.8	0.7	1.8
Unidentified Birds	5.9	4.8	4.6	3.6	4.6
Total Birds	8.0	7.8	6.4	4.3	6.4
Frogs	0	0.6	0.5	0	0.2
Lizards	9.0	3.6	4.1	0	3.8
Number of Vertebrates	187	168	218	278	851
Number of Feces	240	222	186	242	890
Percentage Feces With					
Beetles	56.7	59.5	40.8	10.3	41.8
Scorpion	0.8	2.3	1.6	0	1.2
Seeds	0	0	1.6	0.8	0.6
Vegetation	5.0	9.5	7.0	6.6	7.0
Berberis buxifolia	0.8	14.9	14.0	0.4	7.5
Egg shells	4.6	4.5	4.3	0	3.4
Mean Mass of Vertebrate Prey (kg)	2.20	2.32	1.97	2.21	2.17

Table 2.--Seasonal percent occurrence of vertebrate prey and percentage of feces with invertebrate remains determined from culpeo fox feces collected in Torres del Paine National Park, Chile, 1985-1989.

Prey items	Sep-Nov	Dec-Feb	Mar-May	Jun-Aug	Total
Rodentia					
Akodon spp.	4.8	8.5	8.4	5.2	6.6
Auliscomys micropus	1.6	6.8	4.7	2.2	3.7
Chelemys macronyx	1.1	0	0.5	0	0.4
Eligmodontia typus	0	0.6	0	0	0.1
Euneomys chinchilloides	0	1.1	0.5	0.4	0.5
Oryzomys longicaudatus	5.4	3.4	5.3	6.1	5.1
Phyllotis darwini	0	0.6	1.1	0.4	0.5
Reithrodon physodes	1.1	2.3	4.2	3.5	2.8
Unidentified	0	1.7	1.1	0	0.6
Total Rodents	14.0	25.0	25.8	17.8	20.3
Lagomorpha					
Lepus capensis	75.9	59.9	66.8	70.4	68.5
Carnivora					
Conepatus humboldti	0	1.1	1.1	0.9	0.8

Table 2. (continued)

Artiodactyla					
Bos	0.5	0	0.5	0.9	0.5
Lama guanicoe	1.1	2.3	0.5	2.6	1.7
Ovis aries	0.5	1.1	1.1	0.9	0.8
Total Ungulates	2.1	3.4	2.1	4.4	3.0
Total Mammals	92.0	89.4	95.8	93.5	92.6
Birds					
Chloephaga picta	6.4	6.2	3.7	4.4	5.1
Unidentified Birds	1.1	3.9	0.5	1.7	1.8
Total Birds	7.5	10.1	4.2	6.1	6.9
Lizards	0.5	0.5	0	0.4	0.5
Number of Vertebrates	187	177	190	230	784
Number of Feces	158	140	159	188	645
Percentage Feces With					
Beetles	0.6	4.3	1.9	1.1	2.0
Vegetation	3.2	2.9	3.1	2.1	2.8
Berberis buxifolia	0	2.9	0.6	0.5	1.0
Egg shells	0.6	2.1	0	0	0.7
Mean Mass of Vertebrate Prey (kg)	2.81	2.41	2.45	2.66	2.59

Table 3.--Seasonal estimates of small rodent numbers (± SE) in Torres del Paine National Park, Chile. Values are the mean of three monthly estimates calculated by using the Fourier estimator of Program Capture (White et al., 1978). Habitat and seasonal means followed by the same letter are not significantly different ($P > 0.05$). Values followed by an asteric are the mean of the number of distinct individuals (N_{t+1}) captured each month and were not used in statistical tests.

	Upland Grassland	Shrub Transition	Mata Negra	Matorral Shrubland	Nothofagus Thicket	By Season
Spring	0 ± 0 *	0.7 ± 0.3*	14.3 ± 1.9	29.3 ± 1.8	16.0 ± 5.0	19.9 ± 2.9a
Summer	0 ± 0 *	2.0 ± 1.5*	14.0 ± 1.7	31.0 ± 3.5	17.7 ± 4.2	20.9 ± 3.1a
Fall	0 ± 0 *	7.0 ± 0.6*	21.7 ± 1.3	28.5 ± 3.5	38.3 ± 7.4	29.6 ± 3.8
Winter	0.3 ± 0.3*	3.7 ± 1.2*	17.0 ± 2.0	23.5 ± 6.5	17.3 ± 6.6	19.0 ± 3.1a
By habitat			16.7 ± 1.3a	28.5 ± 1.7b	22.3 ± 3.8ab	

Table 4.--Mean (± SE) number of beetles (Coleoptera) caught in pitfall traps from October, 1987, through March, 1988, in Torres del Paine National Park, Chile. Habitat and monthly means followed by the same letter are not significantly different ($p > 0.05$).

	Upland Grassland	Shrub Transition	Mata Negra	Matorral Shrubland	*Nothofagus* Thicket	By Month
October	23.2 ± 3.5	67.8 ± 13.8	41.0 ± 17.0	25.6 ± 6.6	15.6 ± 3.1	34.6 ± 5.7a
November	45.6 ± 9.4	65.8 ± 7.8	23.6 ± 8.7	24.2 ± 3.9	28.8 ± 8.0	37.6 ± 4.6a
December	28.2 ± 8.1	28.6 ± 4.0	12.6 ± 2.8	21.8 ± 2.9	26.8 ± 5.5	23.6 ± 2.4
January	21.0 ± 3.6	13.4 ± 2.0	11.0 ± 2.9	11.2 ± 1.5	9.4 ± 2.0	13.2 ± 1.3b
February	3.8 ± 2.2	12.2 ± 3.5	2.2 ± 0.6	2.0 ± 0.3	2.6 ± 0.7	4.6 ± 1.1bc
March	2.8 ± 1.1	3.2 ± 1.3	0	1.2 ± 0.5	2.6 ± 0.9	2.0 ± 0.4c
By habitat	20.8 ± 3.4a	31.8 ± 5.4	15.1 ± 3.9a	20.8 ± 3.4a	14.3 ± 2.5a	

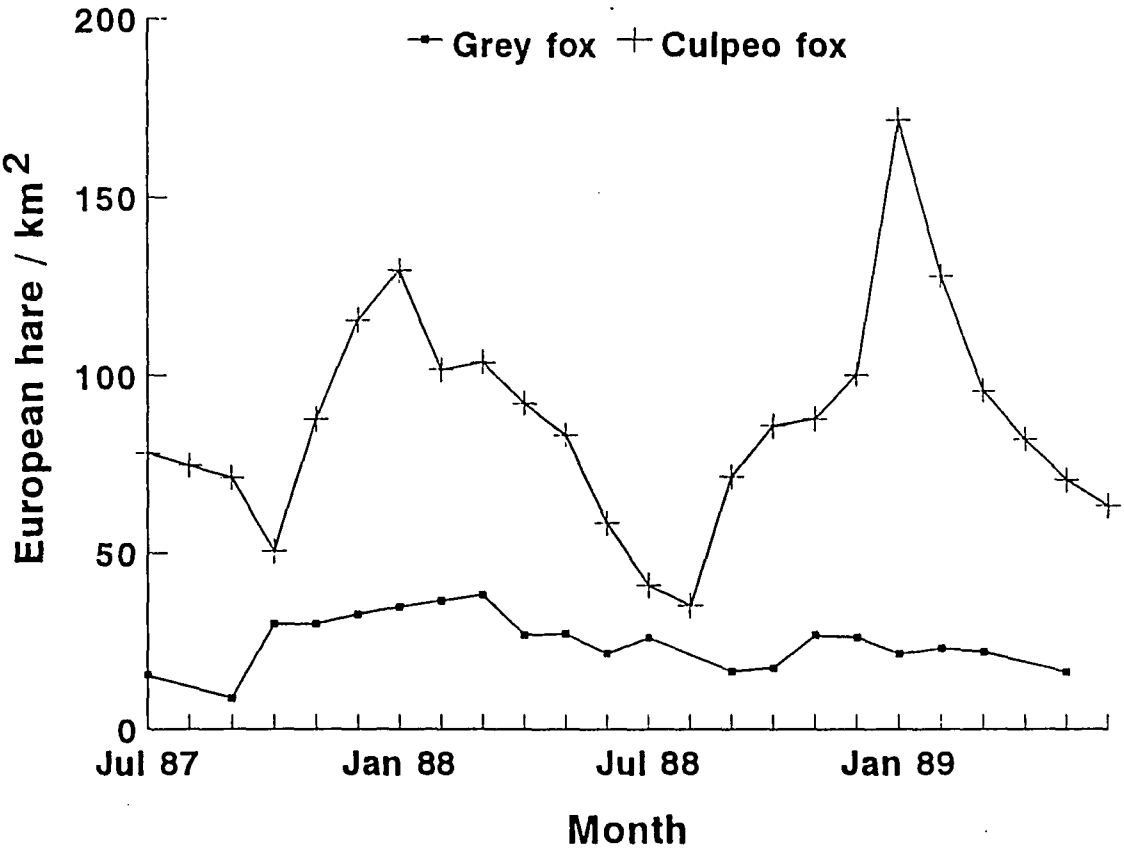

Fig. 1.--Seasonal densities of European hare in South American grey and culpeo fox distribution areas, determined from monthly estimates from July, 1987, to June, 1989, from line transects as calculated by using the Fourier series estimator in Program TRANSECT (Burnham et al., 1980).

SECTION 3.

PARTITIONING OF SPATIAL AND TEMPORAL RESOURCES BY SYMPATRIC *DUSICYON GRISEUS* AND *D. CULPAEUS* IN THE PATAGONIA OF SOUTHERN CHILE

PARTITIONING OF SPATIAL AND TEMPORAL RESOURCES BY SYMPATRIC *DUSICYON GRISEUS* AND *D. CULPAEUS* IN THE PATAGONIA OF SOUTHERN CHILE

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Running Head: Resource Partitioning

SUMMARY

(1) The activity patterns, local distribution, and habitat utilization of sympatric South American grey fox (Dusicyon griseus) and culpeo fox (D. culpaeus) were studied in eastern Torres del Paine National Park, Chile, to determine if the two species partition spatial and temporal resources. Forty-four grey and 19 culpeo fox were captured from January 1986 through March 1989 and monitored by using radio telemetry techniques.

(2) Both grey and culpeo fox were primarily nocturnal. Mean daily activity did not differ between species or among seasons, but grey fox had a greater mean daily activity rate in summer and fall and the mean daily activity rate for culpeo fox was greater in winter and spring.

(3) Seasonal and annual home ranges of culpeo fox were significantly larger than those of grey fox, but did not differ between sexes or among seasons. Home ranges of grey and culpeo fox were interspersed in a mosaic-like arrangement, but did not overlap.

(4) There were significant differences between grey and culpeo fox use of habitat types and vegetation density categories. Grey fox were located significantly more often in upland shrub transition habitat and in areas of medium cover density. Culpeo fox were found significantly more often in thickets of trees and in areas of high density. Habitat use

was related to availability; matorral shrubland or Nothofagus thicket habitat was selected for by all culpeo fox and by 60% of grey fox tested.

(5) Interference competition by culpeo fox or exploitation competition may have been important in determining fox distribution in these distinct habitats.

Key-words: activity patterns, distribution patterns, habitat utilization, resource partitioning, Patagonia

INTRODUCTION

Culpeo (Dusicyon culpaeus) and South American grey fox (D. griseus) are found east and west of the Andes from northern Chile and Argentina south to Tierra del Fuego (Osgood 1943; Crespo 1975; Ginsberg & Macdonald 1990). The two species become more sympatric toward the southern part of their ranges, perhaps because there is less opportunity for altitudinal separation as the Andes decrease steadily in elevation toward southern Chile (Fuentes & Jaksic 1979).

Although both species have been well studied in comparison with other South American canids (reviewed by Medel & Jaksic 1988; Ginsberg & MacDonald 1990), habitat preferences and activity patterns are almost unknown for the two species (Greer 1965; Miller & Rottmann 1976; Fuentes & Jaksic 1979). Both species are reported to occupy open habitats in plains, pampas, and low mountains, although in the Patagonia culpeo fox may use wooded areas more and open habitat less than grey fox (Duran, Catlan & Yañez 1985; Jaksic, Schlatter & Yañez 1980).

Grey and culpeo fox diverged only 250,000 years ago (Wayne & O'Brien 1987; Wayne et al. 1989). For these two closely related carnivores to coexist, ecological theory predicts that they will partition their resources, thereby reducing competition (Rosenzweig 1966). The degree of competition between two species may be related to differences

in body sizes (Pacala & Roughgarden 1985, Moulton & Pimm 1986). Fuentes & Jaksic (1979) used an extension of this argument to postulate that grey and culpeo fox are increasingly divergent in size at southern latitudes as a result of competition caused by increased sympatry between the two species. Fuentes and Jaksic attempted to demonstrate that competition was reduced by partitioning of prey resources, but they were unable to correlate fox body size differences to variations in mean size of potential prey species. The researchers did not, however, address the possibility that in addition to, or instead of partitioning food resources, the two species may demonstrate spatial and temporal differences in habitat use.

This study compares the behavioral ecology of sympatric populations of grey and culpeo fox. The objectives were to analyze their patterns of activity, local distribution, and habitat utilization and to evaluate how they partition their resources in time and space. It was predicted that either grey and culpeo fox would partition habitat resources spatially and have nonoverlapping home ranges or that home ranges overlapped, and foxes would have spatial or temporal differences in habitat utilization.

STUDY AREA

The study was conducted from 1986 through 1990 in the eastern foothills of the Andean mountain range in southern Chile. The 21,000-ha study area was located in the eastern part of Torres del Paine National Park (51°3'S, 72° 55'W), between the Park's border to the east, Lago Pehoe to the west, and Laguna Cebolla and Lago Sarmiento to the north and south. The Park encompasses 2,400 km^2 and provides almost undisturbed habitat for wildlife.

Plant associations and habitats within the park are very heterogeneous, ranging from glacier-covered mountains to dense Nothofagus deciduous forest and grassland. Approximately 70% of the Park consists of a steppe biome, or pre-Andean, dry shrub association, and the remainder is a mosaic of lakes, forests, and arid-mountain alpine zones. The steppe is characteristic of the southern South America pampa found in Chile and Argentina at elevations below 500 m (Pisano 1973, 1974).

The study area can be separated into several recognizable habitats on the basis of dominant plant species and vegetative structure. Upland grassland includes the vega (wet meadow), coirón (bunch grass), and hierba (forb) communities described by Ortega & Franklin (1988). Dominant grass species of this habitat are Festuca gracillina, Anarthrophyllum patagonicum,

and F. palliscens, in order of decreasing cover (Pisano 1973, 1974; Texera 1973; Ortega & Franklin 1988). Upland shrub transition habitat is a continuum from grassland to dense, continuous stands of low shrubs < 1 m high. The locally dominant shrub species is "mata barrosa" (Mulinum spinosum), a spiny, dome-shaped shrub, common in thin, rocky upland. Other common shrub species are "senecio" (Senecio patagonicus), "calafate" (Berberis buxifolia), and "paramela" (Adesmia boronoides). Mata negra transition habitat is also a continuum from grassland to bushes, but is dominated by "mata negra" (Verbena tridens), a 1- to 1.5-m shrub often covering large areas in thick, almost impenetrable stands. Matorral shrubland is a varied, more dense habitat, often containing many of the species common in upland shrub transition and mata negra transition habitats, but also including low woody vegetation averaging around 1.5 m. Characteristic trees or tall shrubs of this habitat are Nothofagus pumilio, Escallonietum rubrum, and Embothrium coccineum. Plant species of Nothofagus thicket habitat are often the same as those in matorral shrubland, but they are found in larger stands of taller trees (rarely > 10 m), with a more open understory.

Data were separated into four, 3-month climatic periods, or seasons, based on temperature, precipitation, and wind. Summer (December - February) is windy, rainy, and relatively warm (January mean daily temperature is 12.6°C). Winter (June

- August), is dry, less windy, and relatively cold (mean daily July temperature is 0.2°C) (temperatures from records obtained from 1985 to 1987 at park headquarters). Spring and fall temperatures were intermediate and wind patterns were less predictable.

Mean annual precipitation is 550 mm, with 60% falling from January to May (Pisano 1974). Adjacent mountains and ice fields create local weather patterns, reflected by a large variability in precipitation (Pisano 1974).

METHODS

Foxes were captured in padded leg-hold traps (Victor No. 1½ soft-catch coil spring) and either immobilized with ketamine hydrochloride (Ramsden, Coppin & Johnston 1976) administered intramuscularly (approximate dosage: 25 mg/kg body wt) or handled without drugs after muzzling the jaws and securing the legs. Each fox was sexed, aged, weighed, measured, tagged in both ears with numbered plastic eartags, and fitted with a motion-sensitive radiocollar (164 Mhz; Advance Telemetry Systems Inc., Bethel, Minnesota, USA). Weights and body measurements are reported as mean ± standard error. Extra efforts were made to capture foxes in parts of the study areas without marked foxes, to ensure that the study area was evenly covered.

Locations (2064 daytime, 430 nighttime) were recorded nonsystematically two to four times a week by using a Yagi three-element, directional antenna and portable receiver (AVM Instrument Company) and locations were recorded on aerial photos (1:16,000). Fewer nighttime locations were recorded because the terrain made them difficult to determine without compromising observer safety and without influencing fox movements. Rapid habituation of grey and culpeo fox to observers, because of the protected status of the foxes in the National Park, facilitated relocating tagged foxes, and they were almost always located by circling within 10-20 m of the

fox to accurately determine location and habitat characteristics. Formal analyses of location error were unnecessary because of the short distances from which foxes were located. Forty-six percent of all locations were visually confirmed. Habitat at each location was classified as 1) exposed rocks and unvegetated soil, 2) upland grassland, 3) upland shrub transition (grass and shrubs < 1 m high), 4) mata negra transition (mata negra and shrubs < 1 m), 5) matorral shrubland, and 6) Nothofagus thicket. Density of the vegetation, or an estimate of the visual obstruction provided to a fox, was characterized at each location as the percentage vegetative cover from ground level to a height of 30 cm. Analogous to using a cover board (Nudds 1977), percentage vegetative cover was categorized subjectively as high (75 - 100%), medium (26 - 74%), or low (0 - 25%).

Spatial Distribution Patterns

Home-range size was estimated seasonally (1 September to 28 February and 1 March to 31 August) and annually (1 September to 31 August). Home ranges of adult resident foxes were calculated on the basis of a minimum of 20 and a mean of 45 locations (for each 6-month period), with minimum convex polygon (Mohr 1947) and 95% harmonic mean estimators (Dixon & Chapman 1980) by using program DC80 (Carey, University of Wisconsin, USA, pers. commun.). Young, transient, or

displaced foxes were not included in this analysis. Data were analyzed with programs BIOCHECK and BIOPLOT (White & Garrott 1990) and individual observations were discarded if they seemed to be errors or excursions outside the normal home range (Burt 1943).

Minimum convex polygons (MCP) were used so that results could be compared with other studies. Although this method is strongly influenced by outliers and by number of observations (Jennrich & Turner 1969, White & Garrott 1990), it is one of the most widely used home-range estimators. The 95% harmonic mean (HM), a nonparametric estimator, was used because it does not make assumptions of home-range shape and is less biased by and less susceptible to influence of outliers and multiple activity centers than other parametric estimators (Boulanger & White 1990; White & Garrott 1990). Because home-range estimates were based primarily on daytime locations (and may be biased low) and because assumptions of home-range models often are difficult to meet, these values were used primarily as indices to test whether home-range size differed by species, sex, and season and secondarily as broad comparisons with other studies. Natural-log transformations were used to improve distributions of home-range estimates. Analysis of variance (PROC GLM, SAS Institute Inc. 1989) was used to test for significant differences in home-range sizes calculated between species and sexes and among annual and seasonal time

periods.

To determine overlap of seasonal home ranges among foxes, locations were plotted on maps and compared visually. Overlap between adjoining pairs of home ranges also was measured quantitatively by using program MRPP (Mielke & Berry 1982). Although this estimate has a very conservative criterion for overlap (small differences greatly affect the estimate of overlap), it was used because it is a nonparametric approach comparing the utilization distributions of the two data sets (White & Garrott 1990).

Habitat Utilization Versus Availability

The relationship of habitat type to species, season, and activity level and the relationship of vegetation density category to species, season, and activity level were assessed using Log-linear analyses (Dixon 1981, Sokal and Rohlf 1981). Only data from individual foxes with 20 or more observations of locations were used in these analyses. Terms used in the resulting models reflect significant relationships within the data. Observations on an individual fox were not completely independent, therefor Chi-square values for each term in the model were corrected to insure conservative estimates of significance. Corrected Chi-square values were calculated by dividing the Chi-square values by the average design effects (Rao and Scott 1981). The average design effect is a measure

of the lack of complete independence of the observations on each animal and is the mean of the design effects of each of the parameter estimates of the multinomial logistic function. Average design effects were determined using Program PC CARP (Statistical Laboratory, Iowa State University).

Differences in use of habitat type and vegetation density between grey and culpeo fox were tested also by Chi-square analysis controlling for season and activity (PROC FREQ, SAS Inst. 1989). Once a significant relation was established, individual Chi-square values of each habitat type or vegetation density category were compared with Bonferroni normal statistics to examine the item's influence (Neu et. al. 1974; Johnson & Wichern 1982:197). Differences were considered significant when individual Chi-square scores had an alpha level less than 0.05/number of categories.

Differences in habitat selection between grey and culpeo fox were compared by using adults for which there were at least 50 observations of habitat utilization and which had home ranges they had occupied for at least a year. To ensure statistical independence of individual animals used in this analysis, only one fox was used if both members of a pair were marked. Availability of the six habitat categories was estimated at 500 random points within home ranges of 7 culpeo and 12 grey fox. Fifty points were distributed 10 paces apart on 10 parallel transects started at random along a baseline

crossing the entire home range. Selectivity of habitat categories by each fox was tested by using the Chi-square test of homogeneity and Bonferroni confidence intervals (Marcum & Loftsgaarden 1980). The results were presented as the percentage of foxes selecting for or against a habitat category at a $P < 0.0083$ (0.05/number of categories) level of significance.

Activity Patterns

Diel cycles in activity patterns were assessed by monitoring all radio-collared foxes from prominent hills by using either the Yagi antenna or an omnidirectional whip antenna mounted 3 m above the ground on a vehicle. Samples of activity were taken randomly during 4- to 36-hr continuous observation periods, and no more than one sample per individual was taken per hour. The relationships among hour-interval, activity level, species, and season were assessed by using log-linear analyses (Dixon 1981, Sokal and Rohlf 1981) of data from individuals for which two or more activity readings were recorded for each hour-interval.

The proportion of the observations each individual was active (percentage activity) was calculated seasonally for each of the 24 1-hour intervals. Hour-intervals for each individual had to have at least two activity readings and a minimum of 20 hour-intervals per day were required for an

animal's percentage of activity to be included in analyses. Average daily activity levels of each individual were estimated from unweighted mean percentages of activity for all 24 one-hour activity periods. Differences in mean daily activity levels among seasons and between species were tested by using log-linear analysis (Dixon 1981, Sokal and Rohlf 1981).

RESULTS

Forty-four grey (23 males and 21 females) and 19 culpeo fox (11 males and eight females) were captured from January 1986 through March 1989. Adult grey fox males weighed significantly more than females (mean ± SE; 3.98 ± 0.09 versus 3.34 ± 0.11 kg; $\underline{t}$ = 4.43, 29 df, $P < 0.0001$) and had longer hind feet (138 ± 2 versus 132 ± 2 mm; $\underline{t}$ = 2.13, 31 df, $P = 0.04$), but were not significantly different in body length (661 ± 23 versus 679 ± 39 mm, 31 df, $P = 0.69$). Adult culpeo fox males also significantly outweighed females (11.65 ± 0.78 versus 7.82 ± 0.55 kg; $\underline{t}$ = 4.02, 6 df, $P = 0.007$), had longer hind feet (177 ± 4 versus 155 ± 3 mm, 6 df, $P = 0.004$), and were not significantly different in body length (1064 ± 105 versus 960 ± 121 mm, 6 df, $P = 0.54$).

Spatial Distribution Patterns

Home-range sizes were determined for eight adult culpeo fox (four males and four females) and 20 adult grey foxes (ten males and ten females). Home-range sizes were analyzed independently where there was more than one seasonal or yearly area of use per fox, resulting in a total of 36 grey foxes (18 female and 18 male) and 20 culpeo foxes (ten female and ten male) seasonal home ranges and 23 grey foxes (11 female and 12 male) and 15 culpeo foxes (seven female and eight male) annual home range estimates.

Seasonal home-ranges, as indexed by both home-range estimators, varied significantly by species (MCP: $F = 11.54$, 1 df, $P = 0.001$; HM: $F = 15.69$, 1 df, $P < 0.001$). Mean (± SE) seasonal culpeo fox home ranges were 3.5 ± 0.6 km^2 as measured by MCP, and 7.7 ± 1.4 km^2 as calculated by HM compared with 1.7 ± 0.2 km2 (MCP) and 3.2 ± 0.5 km^2 (HM) for grey fox (Table 1). Patterns of annual home ranges were similar. Annual home ranges varied by species (MCP: $F = 8.32$, 1 df, $P = 0.008$; HM: $F = 17.43$, 1 df, $P < 0.001$). Mean annual home ranges were 4.5 ± 0.6 km^2 (MCP) and 9.8 ± 1.6 km^2 (HM) for culpeo fox and 2.0 ± 0.2 km^2 (MCP) and 2.9 ± 0.3 km^2 (HM) for grey fox. Neither seasonal nor annual home ranges varied by sex, and seasonal home ranges did not differ significantly between spring-summer and fall-winter periods for either species ($P > 0.05$ for all comparisons).

A visual comparison of the home-range distributions of grey and culpeo fox clearly revealed that home ranges were interspersed in a mosaic-like arrangement, but they did not overlap (Fig. 1). This was confirmed by results of program MRPP, which rejected in all cases the null hypothesis of overlap at high levels of significance ($P < 0.001$). Overlap in areas of use, except by individuals of a breeding pair, was documented only twice, and both incidents were related to long movements. A male culpeo fox made a foray of about 15 km in

three days through several culpeo and grey fox home-ranges before returning to his original area, and a male grey fox, displaced by a neighboring grey fox male, crossed a large river and two culpeo fox home ranges before establishing a new home range 12 km from his old one.

Habitat Utilization Versus Availability

Log-linear analysis revealed significant differences between species (F) in their use of habitat (H), but not in species use of habitat among seasons (S) or between activity (A) levels ($\ln f_{(ijkl)} = H_i + F_j + S_k + A_l + HF_{ij}$; HF_{ij}: adjusted $G = 127.69$, 5 df, $P < 0.001$). Average design effect for the parameters of the habitat utilization model was 5.9, indicating that almost six observations of habitat utilization were necessary to obtain the equivalent of one independent observation. There were also significant differences between species in their use of vegetation density categories (D), but not in their use of vegetation density categories among seasons or between activity levels ($\ln f_{(ijkl)} = D_i + F_j + S_k + A_l + DF_{ij}$; DF_{ij}: adjusted $G = 51.68$, 2 df, $P < 0.001$). Average design effect for the parameters of the vegetation density model was 3.8.

These variations between grey and culpeo fox use of habitat and vegetation density categories were confirmed by

Chi-square analyses. Grey and culpeo fox (controlling for season and activity) differed in use of habitat type ($\underline{X}^2$ = 745.6, 5 df, $P < 0.001$) and vegetation density category ($\underline{X}^2$ = 193.2, 2 df, $P < 0.001$). Grassland ($\underline{X}^2$ = 84.9, $P < 0.001$), shrub transition ($\underline{X}^2$ = 139.6, $P < 0.001$), mata negra ($\underline{X}^2$ = 82.6, $P < 0.001$), and tree habitat ($\underline{X}^2$ = 441.1, $P < 0.001$) contributed the most to differences in habitat use for the two species (Table 2 and 3).

Grey and culpeo fox displayed similar patterns of habitat selection (Table 4). All seven culpeo fox and seven of twelve (58%) grey fox selected either for matorral shrubland or for Nothofagus thicket habitat within their home ranges. Upland grassland habitat was selected against by two (29%) of the culpeo fox and by two (17%) of the grey fox.

Activity Patterns

We collected 7278 hourly activity readings for grey fox (1506 in spring, 1755 in summer, 2186 in fall, and 1831 in winter) and collected 6032 for culpeo fox (1235 in spring, 983 in summer, 1682 in fall, and 2132 in winter). Both grey and culpeo fox were primarily nocturnal (Fig. 2). Log-linear analysis revealed there was not a significant association between fox species and activity ($G = 0.18$, 1 df, $P = 0.67$) but that there was a significant interaction between fox

species the other two terms of the model, hour-interval (H) and season ($ln_{(ijkl)} = A_i + F_j + H_k + S_l + AH_{ik} + AS_{il} + AFH_{ijk} + AFS_{ijl} + AHS_{ikl}$; AH_{ik}: G = 1855.77, 23 df, P < 0.001; AS_{il}: G = 21.16, 3 df, P = 0.001; AFH_{ijk}: G = 107.34, 23 df, P < 0.001; AFS_{ijl}: G = 35.42, 2 df, P < 0.001; AHS_{ikl}: G = 463.87, 69 df, P < 0.001.

Mean daily activity did not differ between species or among seasons, but there was a significant interaction between species and seasons (G = 14.5, 3 df, P < 0.001), with grey fox having a greater mean daily activity rate in summer and fall and culpeo fox having a greater mean daily activity rate in winter and spring. Throughout the year, grey fox were active 43% of the time and culpeo fox activity level was 41%.

DISCUSSION

Spatial Distribution

Spatial selection can occur at several levels (Wiens 1973; Johnson 1980). Because grey and culpeo fox are sympatric in Torres del Paine National Park, first-order selection, or the selection of a geographic range, is similar in this area for grey and culpeo fox. But, second-order selection, or the selection of a home range within their geographic range, differed.

Instead of using the same areas and partitioning the resources available within overlapping home ranges, grey and culpeo fox were spatially segregated. This indicates that the two species either mutually avoided each other or that one actively excluded the other. Because of its size advantage and aggressiveness, we believe that culpeo fox are dominant over grey fox and that spatial separation is maintained by a combination of avoidance by grey fox and aggression by culpeo fox.

The spatial arrangement of pairs of grey and culpeo fox suggests that they maintain year-around home ranges. No intraspecific interactions were observed between grey and culpeo foxes. The only two observations of direct interactions, both aggressive, occurred during the breeding season (August and September). In one instance, two grey fox males passed within 15 m of each other, one growling with its

back arched and chin lowered; in the other instance, the resident grey fox female made a brief attack and then a 50-m chase after a second female.

Activity Patterns

Although temporal partitioning of resources was not important for grey and culpeo fox because of their spatial segregation, there were some differences in their diel patterns that may have been related to differences in food habits and foraging behavior. Although both species were essentially nocturnal, grey fox were more active during the day than culpeo fox. Grey fox daytime activity was probably related to their greater reliance on beetles and scavenging of carcasses (see Section 3). Culpeo fox patterns may have been affected by the activity patterns of European hare (Lepus capensis) and small rodents, which were its two principal prey. Activity patterns also could have been influenced by other competitors. Great-horned owl (Bubo virginianus), like culpeo fox, is a nocturnal predator that preys heavily on small rodents and European hare (Iriarte et al. 1990). Threat of predation was unlikely to modify activity, except on isolated occasions, because puma (Felis concolor), the main predator on grey and culpeo fox, were too few and dispersed and fed principally on other species (Iriarte et al. 1991).

Our findings differ from those of Jaksic, Schlatter &

Yañez (1980), who concluded from indirect evidence based on behavioral patterns of grey and culpeo fox prey that these fox are crepuscular. This difference in activity patterns between the two foxes in central Chile and the foxes in southern Chile may possibly be caused by differences in the activity patterns of their prey, but is more likely an artifact of making inferences from the ecology of the prey species and not directly from the behavior of the foxes.

Habitat Utilization

Grey and culpeo fox were distributed in different habitats. Grey fox occupied open grassland mixed with occasional patches of taller, more dense vegetation; and culpeo fox inhabited the transition zones between matorral shrubland and Nothofagus forests. Because grey and culpeo fox had spatially separated home ranges, interference competition by culpeo fox or exploitation competition may have been important in determining fox distribution in these distinct habitats. If culpeo fox were absent, grey fox might have a much wider local distribution, utilizing the more wooded and densely vegetated areas now occupied by culpeo fox.

There are two lines of evidence supporting the contention that habitat utilization was influenced by competitive pressures. Selection of various habitat components within home ranges of grey and culpeo fox was similar. Although

available habitat within home ranges of grey and culpeo fox was different, a large percentage of both species selected for Nothofagus thicket and matorral shrubland habitat. This shows that both species are spending a greater proportion of their time in these habitats than would be expected from the habitat's availability within their home ranges, perhaps because these areas have greater densities of European hare and small rodents than other habitats (see Section 3) and because these habitats provide more cover for resting and den sites.

Historical records from Torres del Paine National Park also support the hypothesis that the distribution of grey and culpeo fox in different habitats results in part from competition between the two species. In several areas of the park, grey fox are now found where only culpeo fox were reported previously (Abello 1979). Since the termination of sheep grazing in the Park, the only vegetational change has been an increase in amount of matorral shrubland which should have favored culpeo fox.

Because grey and culpeo fox both are able to adapt to a wide continuum of habitats from grasslands to more closed forests and both seem to select for similar habitat types or structures within their home ranges, habitat availability alone does not seem to be determining fox distribution patterns. Other factors, such as food availability and energy

demands, may be more important than habitat type in determining fox distribution patterns (see Section 4). As population densities of prey change, especially of the European hare, we expect to see continual shifts in the distributions of grey and culpeo foxes in Torres del Paine National Park.

ACKNOWLEDGMENTS

We thank the Chilean National Forestry and Park Service (CONAF) for their assistance and collaboration. We give special thanks to the personnel of Torres del Paine National Park for their help, especially Park superintendent Guillermo Santana and Park guards Oscar Guineo, Francisco Barrientos, and Juan Toro. We appreciate the dedicated field work of Gabriel Arribillaga, Fredy Barrientos, Gail Blundell, Jill Bright, Steve Catir, Lloyd Christian, Kyle Harms, Judith Hoffman, Agustin Iriarte, Andy Phillips, Barry Samson, and Steve Wilson, as well as the invaluable advice of Todd Fuller. Earlier drafts were improved by Michael Behl, Lou Best, William Clark, and Irv Klaas. Kenneth Koehler provided invaluable statistical advice. This study was made possible by grants from the National Geographic Society (Grant No. 3581-87), Patagonia Research Expeditions (Iowa State University), the Organization of American States, the International Telephone and Telegraph Corporation Fellowship Program, and the National Wildlife Federation. This project was conducted under a research agreement (Proyecto Puma) between Iowa State University and the Chilean National Forestry and Park Service. Journal Paper No. J-14872 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2519.

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Table 1. Mean sizes (± SE km^2) of 36 South American grey foxes (18 female and 18 male) and 20 culpeo foxes (10 female and 10 male) seasonal home ranges and 23 grey foxes (11 female and 12 male) and 15 culpeo foxes (7 female and 8 male) annual home ranges from 1986 to 1989 at Torres del Paine National Park, Chile. Calculations based on resident adults for which a minimum of 20 and a mean of 45 observations were recorded for each 6-month period.

	Minimum Polygon		95% Harmonic Mean	
	Grey	Culpeo	Grey	Culpeo
Seasonal				
Male	1.6 ± 0.3	4.6 ± 0.8	2.7 ± 0.5	9.0 ± 2.2
Female	1.7 ± 0.3	2.4 ± 0.6	3.7 ± 0.9	6.4 ± 1.9
Combined	1.7 ± 0.2	3.5 ± 0.6	3.2 ± 0.5	7.7 ± 1.4
Annual				
Male	2.2 ± 0.4	5.4 ± 0.9	2.9 ± 0.5	11.1 ± 2.2
Female	1.8 ± 0.3	3.4 ± 0.8	2.8 ± 0.5	8.2 ± 2.3
Combined	2.0 ± 0.2	4.5 ± 0.6	2.9 ± 0.3	9.8 ± 1.6

Table 2. Percentage habitat use of South American grey and culpeo fox when inactive and active and at different cover densities from 1986 through 1990 in Torres del Paine National Park, Chile.

	Grey fox			Culpeo fox		
	Inactive	Active	Total	Inactive	Active	Total
Habitat						
Unvegetated	2.7	3.5	2.9	6.7	6.2	6.6
Grassland	13.9	24.9	16.7	1.4	3.1	1.8
Shrub Transition	50.0	47.0	49.3	14.2	18.6	15.2
Mata Negra	10.5	7.0	9.6	25.2	24.9	25.2
Matorral Shrubland	18.5	14.4	17.4	8.9	15.5	10.5
Trees	4.4	3.2	4.1	43.6	31.7	40.7
Cover density						
Low	15.4	14.5	15.2	5.1	6.8	5.5
Medium	49.5	51.9	50.1	24.7	35.4	27.2
High	35.1	33.6	34.7	70.2	57.8	67.3
Number of Locations	1247	428	1679	507	161	671

Table 3. Percentage seasonal habitat use of South American grey fox and culpeo fox from 1986 through 1990 in Torres del Paine National Park, Chile.

	Grey Fox				Culpeo Fox			
Habitat	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Unvegetated	2.5	4.1	2.2	3.2	4.3	6.7	5.1	9.6
Grassland	15.5	12.2	21.5	16.4	0	1.0	4.0	1.8
Shrub Transition	53.4	44.5	47.7	52.1	17.9	15.9	13.1	15.0
Mata Negra	7.6	15.8	7.5	7.7	28.2	28.4	29.0	15.0
Matorral Shrubland	17.6	21.7	15.6	14.3	10.3	12.5	9.1	9.6
Trees	3.4	1.7	5.5	6.3	39.3	35.5	39.7	49.1
Cover Density								
Low	16.6	16.3	15.6	9.8	1.7	6.2	3.4	9.6
Medium	52.9	47.6	31.4	15.5	23.9	28.9	29.1	24.6
High	30.5	36.1	32.1	44.7	74.4	64.9	66.5	65.8
Number of Locations	476	410	505	285	117	208	176	167

Table 4. Percentage of 12 South American grey fox and 7 culpeo fox selecting for and against six habitat categories within their home ranges from 1986 through 1990 in Torres del Paine National Park, Chile.

	Grey Fox		Culpeo Fox	
	% For	% Against	% For	% Against
Habitat				
Unvegetated	-	-	14	-
Grassland	-	17	-	29
Shrub Transition	-	-	-	-
Mata Negra	8	8	29	-
Matorral Shrubland	33	-	29	14
Trees	25	-	86	-

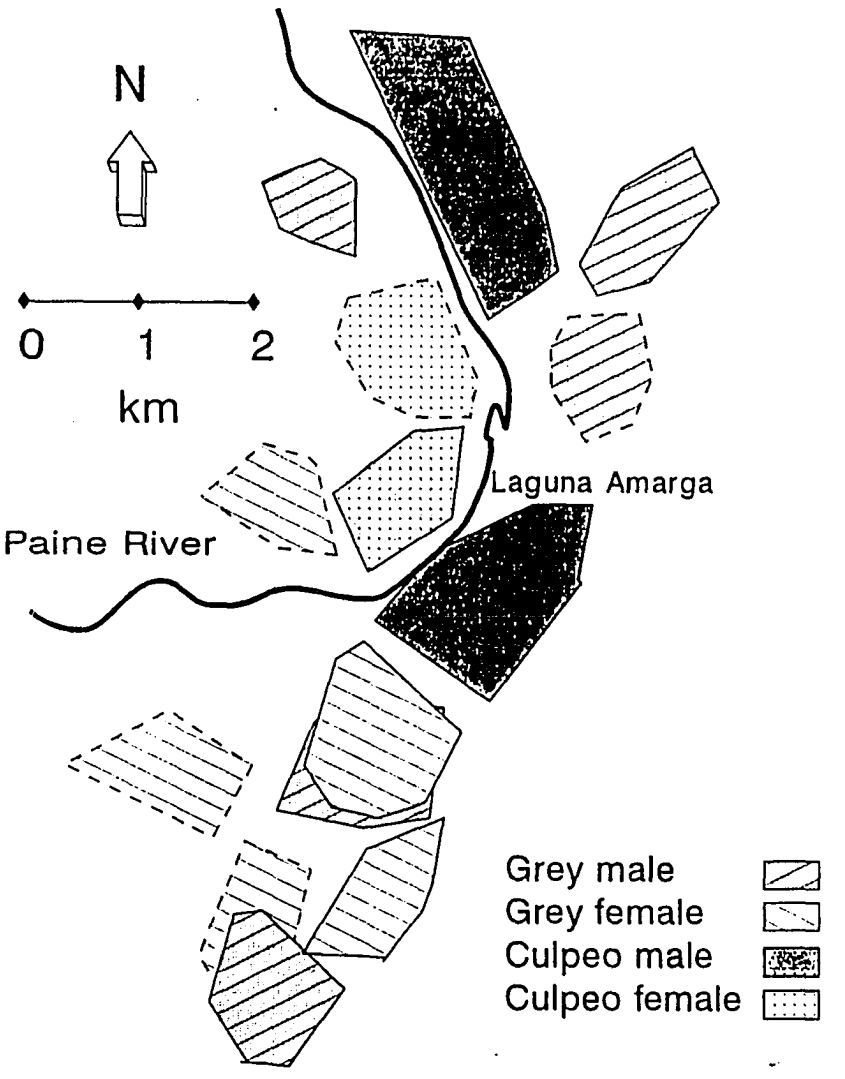

Figure 1. Annual home ranges of South American grey fox (Dusicyon griseus) and culpeo fox (D. culpaeus) from September 1987 through February 1988 in Torres del Paine National Park, Chile. Home ranges outlined in dashed lined are based on less than 20 locations.

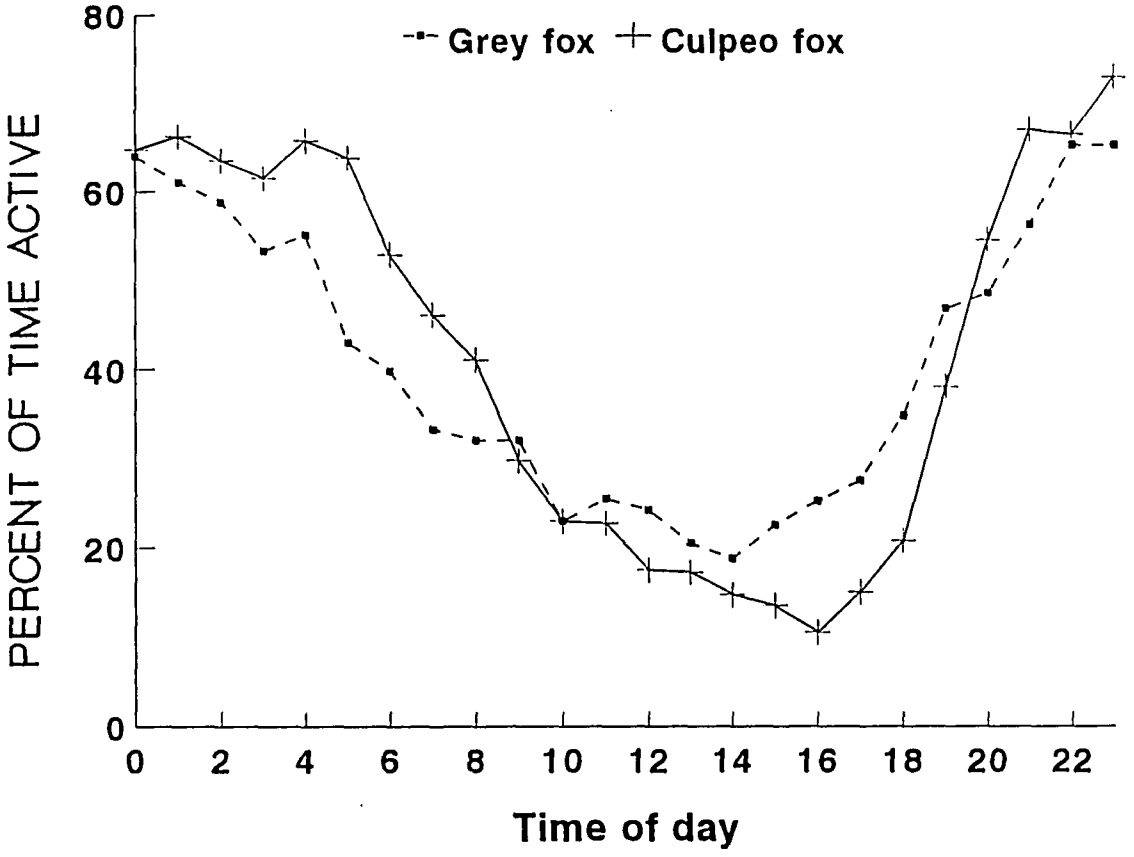

Figure 2. Daily activity patterns of South American grey fox (Dusicyon griseus) and culpeo fox (Dusicyon culpaeus) from 1986 through 1990 in Torres del Paine National Park, Chile.

SECTION 4.

INFLUENCE OF RESOURCE PARTITIONING AND ENERGY REQUIREMENTS ON LOCAL DISTRIBUTIONS OF *DUSICYON GRISEUS* AND *D. CULPAEUS* IN SOUTH AMERICA

Influence of Resource Partitioning and Energy Requirements on Local Distributions of *Dusicyon griseus* and *D. culpaeus* in South America

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Summary. Culpeo (Dusicyon culpaeus) and South American grey fox (D. griseus) have comparable ranges, but the factors determining both their local and geographic distributions are unknown. We compare the behavioral ecology of grey and culpeo fox and review hypothesized factors that determine their distributions when sympatric, and discuss these factors in relation to the foxes geographic distributions. Explanatory hypotheses for distribution patterns which we address are 1) environmental constraints, 2) dietary requirements, 3) habitat requirements, 4) predation or extirpation by humans, and 5) energy requirements. To meet their daily energy requirements, as calculated by theoretical basal metabolic rates, male and female grey fox needed 0.12-0.27 European hares (Lepus capensis) or 7-17 small rodents, compared with 0.4-1.2 European hares or 26-70 small rodents needed to maintain male and female culpeo fox. By examining fox energy requirements, we conclude that the distribution of grey and culpeo fox in southern Chile is determined in part by the distribution and density of the European hare and perhaps, farther north, by the densities of European rabbit (Oryctolagus cuniculus) or medium-sized rodents such as Octodon degus and Abrocoma bennetti.

Key Words: Culpeo fox, South American grey fox, distribution, energy requirements

INTRODUCTION

The culpeo (Dusicyon culpaeus) and South American grey fox (D. griseus) have comparable ranges. Culpeo fox, a medium-sized canid (5-14 kg), is distributed on both sides of the Andes from Ecuador and possibly Colombia south through Peru, Bolivia, Chile, and Argentina to Cape Horn. The smaller grey fox (3-5 kg) has a similar distribution, but its existence in Peru and Ecuador is uncertain and it is found at lower elevations in northern Chile (Osgood 1943; Crespo 1975; Ginsberg and Macdonald 1990). The two species become more sympatric toward the southern part of their range, perhaps because there is less opportunity for altitudinal separation as the Andes decrease in elevation toward southern Chile (Fuentes and Jaksic 1979).

The most detailed knowledge on these foxes relates to their food habits (Medel and Jaksic 1988; see Section 2), with various studies suggesting that both species display opportunism and trophic plasticity. Throughout their range, they depend heavily on small rodents and lagomorphs, but also feed locally and seasonally on lizards, birds, carrion, insects, and berries (Jaksic et al. 1980; Jaksic et al 1983; Johnson 1992; Simonetti et al. 1984; Yañez and Rau 1980). Through most of their distribution, habitat preferences and activity patterns are almost unknown for the two species (Greer 1965; Miller and Rottmann 1976; Fuentes and Jaksic

1979), but evidence suggests they are primarily nocturnal (Iriarte et al. 1989; Johnson 1992). Both species are reported to occupy open habitats in plains, pampas, and low mountains; in Patagonia, however, culpeo fox use wooded areas more and open habitat less than do grey fox (Duran et al. 1985; Jaksic et al. 1980; see Section 3). Although both species have been well studied in comparison with other South American canids (reviewed by Medel and Jaksic 1988; Ginsberg and Macdonald 1990), the factors determining their local and geographic distribution are unknown, in part because of the lack of detailed concurrent studies on both species.

Grey and culpeo fox diverged only 250,000 years ago (Wayne and O'Brien 1987; Wayne et al. 1989) and ecological theory predicts that these two closely related carnivores will coexist by partitioning available resources, thereby reducing competition (Rosenzweig 1966). Because predator body size is often correlated with prey size, body size differences in sympatric predators is frequently used as an indication of the partitioning of prey resources needed for coexistence (see Pimm and Gittleman 1990). This reasoning has been used to explain why grey and culpeo fox are increasingly divergent in size at southern latitudes as they also become more sympatric (Fuentes and Jaksic 1979).

Sympatric grey and culpeo fox in Torres del Paine National Park, located in the southern portion of Chile,

partition available resources spatially. The mosaic arrangement of their exclusive, but inter-mixed, home-ranges suggest that competition determines fox distribution where the two species are sympatric (see Section 3). This spatial segregation of resources implies that, under certain conditions, one species is able to outcompete or exclude the other, which is consistent with the finding that most competitive interactions are asymmetrical, with the effects of one species being clearly greater than the other (Schoener 1983). The dominant species, or superior competitor, is distributed where conditions are favorable and is frequently more strongly limited in numbers or distribution by some factor external to the competitive interaction.

The factors most commonly cited as determining species distribution are 1) environmental constraints such as temperature, precipitation, and other abiotic factors, 2) dietary requirements such as availability of certain prey or category of prey species, 3) habitat requirements such as vegetative structure or distribution, 4) predation or extirpation by humans due to hunting, trapping, or other direct human causes of mortality, and 5) energy requirements.

Species' distributions are limited by tolerances to single environmental factors such as temperature and precipitation or by interactions among several of these factors (Shelford 1908). Fuentes and Jaksic (1979), although

not explicitly, used this fact to theorize that the absence of an altitudinal gradient in southern South America increased sympatry between grey and culpeo fox. Because physical environmental parameters often are correlated with elevation, Fuentes and Jaksic assumed that culpeo fox are better adapted to conditions at higher altitudes and are able to outcompete grey fox there. Where the two fox species are sympatric, as in the Chilean National Chinchilla Reserve in central Chile (Duran et al. 1987) and Torres del Paine National Park in southern Chile, the supposition is that environmental conditions are such that neither species can completely exclude the other.

But environmental factors are unlikely to be the primary factor influencing grey and culpeo fox distribution because both species exhibit a wide tolerance for different climatic regimes. Both have adapted to conditions ranging from the dry, hot climates of northern Chile and Argentina to the strong, cold, seasonal climate of Tierra del Fuego (Redford and Eisenburg 1992). The spatial arrangement of grey and culpeo fox in Torres del Paine National Park in non-overlapping and often intermixed home ranges (see Section 3) is further evidence that environmental constraints alone do not have a strong influence on distributions. It would be very difficult for even localized weather patterns to cause such local distributions.

The distribution of some mammals is dependent on the availability of essential and limited vitamins and minerals. For example, calcium deficiencies leading to nutritional secondary hyperparathyroidism (NSH) can occur in arctic fox and red fox kits consuming meat but having an inadequate ingestion of bones (Van Pelt and Caley 1974; Conlogue et al. 1979). But, such dietary requirements are unlikely to affect the relative distributions of grey and culpeo fox because the two species feed on the same prey and, being closely related, probably have similar nutritional needs. Evidence also suggests that dietary differences between grey and culpeo fox are related as much to variation in prey availability as to differential prey selection (see Section 2).

Differential habitat utilization has been one of the most common explanations for grey and culpeo fox distribution (Fuentes and Jaksic 1979). Even when fox distribution and habitat type are highly correlated, however, this is one of the more difficult hypotheses to discount or prove because habitat characteristics usually correlate with other biotic and abiotic factors such as prey availability and environmental conditions. Because grey and culpeo fox are found both separately and together in a variety of different habitats throughout their geographic range, it is difficult to predict their distribution on the basis of habitat alone.

Observations at Torres del Paine National Park provide

further evidence against a strict relationship between habitat and fox distribution. Most individual culpeo and grey fox selected for Nothofagus thicket and matorral shrubland habitat within their home ranges, in spite of wide variation in the availability of these habitat types (see Section 3). Also, in several areas of the park, grey fox are now found where previously only culpeo fox were reported (Abello 1979; W.L. Franklin personal observation), although the only vegetational change has been an increase in the amount of matorral shrubland, which, according to most accounts, should have favored culpeo fox (see Section 3).

Adult South American grey and culpeo fox do not have any major predators, with the occasional exception of puma (Felis concolor), which are likely to influence distribution. Direct influence of man on grey and culpeo fox distributions through hunting, trapping, and other human-related mortality factors may be responsible for fox distribution patterns in certain parts of their range, especially in densely populated and developed areas such as central Chile (Jaksic et al. 1980) and areas where there are strong local predator-control efforts. The range of grey fox also was extended to Tierra del Fuego by humans; the grey fox was introduced in 1951 in an attempt to control the European rabbit (Oryctolagus cuniculus) (Jaksic and Yánez 1983). In most areas, however, especially in areas less developed, more isolated, or better protected, such as

Torres del Paine National Park, human activities have probably not greatly influenced fox distributions (Miller 1980).

Differential energy requirements of culpeo and grey fox remains as the most likely factor influencing their distribution. Availability of food resources to meet energy requirements can limit species' distribution. Rate of energy expenditure is an important ecological variable because all biologically significant activities require energy which may occasionally be limited, especially in marginal habitats. The objective of this paper is to review the evidence supporting the hypothesis that the distribution of sympatric South American grey and culpeo fox populations in Torres del Paine National Park are determined by energy requirements and discuss this in relation to the geographic distribution of the two predators.

METHODS

Basal metabolic rate (BMR) was used as an index of energy requirements because it correlates well with energy expenditures in the field (McNab 1980). Because BMR is controlled by body mass (Kleiber 1932; Brody and Proctor 1932), and because grey and culpeo fox are sexually dimorphic, we calculated BMR for adult males and females. Adult grey fox males weighed 3.98 ± 0.09 kg (mean ± SE; n = 17), grey fox females weighed 3.34 ± 0.11 kg (n = 14), culpeo fox males weighed 11.65 ± 0.78 (n = 4), and culpeo fox females weighed 7.82 ± 0.55 kg (n = 4).

Recent reevaluation of the factors controlling metabolic rates has shown that, although body mass is the principal factor regulating BMR, a large portion of the variation between calculated and measured BMR can be accounted for by differences in food habits (McNab 1969, 1983, 1986, 1989; but see Harvey et al. 1991). In Torres del Paine National Park, fox yearly diets were significantly different (see Section 2). Mammals accounted for 90% of vertebrate prey items found in grey and culpeo fox feces. European hare (Lepus capensis) was the most common vertebrate found in grey fox feces (45%), with lesser amounts of guanaco (14%) and Akodon species (13%). For culpeo fox, European hare accounted for 69% of the prey items and rodent species accounted for 20%. Grey fox were more omnivorous, feeding more on beetles and plants, especially

from spring through fall. Grey fox had a significantly higher index of standardized vertebrate food-niche breadth than culpeo fox (0.24 ± 0.01 versus 0.09 ± 0.01; T = 10.4, 6 df, P < 0.0001) and a significantly lower mean mass of vertebrate prey (2.17 ± 0.07 versus 2.59 ± 0.09 kg; T = 3.4, 6 df, P = 0.01). Pianka's index of similarity between fox diets was low.

Grey and culpeo fox diets, therefore, differed enough to warrant placing them in different food habit categories. We calculated BMR for culpeo fox by using McNab's (1986) equation for vertebrate-eaters:

$$V\ o_2 / m = 3.08m^{-0.188},$$

where $V\ o_2 / m$ has the units $cm^3*g^{-1}*h^{-1}$ and m is in grams. An equation for carnivores (McNab 1986) intermediate between large invertebrate-eaters and vertebrate-eaters was used for grey fox:

$$V\ o_2 / m = 4.05m^{-0.288}.$$

To convert these equations to kJ/day, we multiplied the results by 24 h/day, by body mass of the sex class, and by the conversion factor 0.02 $kJ/cm^3\ O_2$.

Amount of energy output or total time that an animal can remain active is limited by physiological constraints (Astrand and Rodahl 1977). We determined maximum sustained working level of the two fox species to be equal to four times BMR as

in Drent and Daan (1980). This relationship is supported by Kirkwood (1983), who found the limit in metabolizable energy intake in homeotherms to be equivalent, on average, to 300 to 600% of BMR. Because average daily energy expenditures of large mammals are probably closer to 200 to 300% of BMR most of the year (Robbins 1983), energy requirements based on twice the BMR also were calculated. We used the formula for canidae of Oftedal and Gittleman (1989) as a measure of the impact of reproduction on the energy requirements of females, daily energy deposition during pregnancy (11.92 kJ * kg $^{-0.75}$ * day $^{-1}$), and milk energy output at peak lactation (962 kJ * kg $^{-0.75}$ * day $^{-1}$).

To analyze the role these energy requirements might have on fox distribution, we calculated the number of small rodents and European hare needed to sustain these metabolic rates. The mean body mass of European hare in Torres del Paine National Park was 3350 g (mean weight of 109 hares shot outside but immediately adjacent to the Park during May hunting season) and the body mass of the six most common small rodent species in fox diets averaged 40 g (Iriarte et al. 1990). Although body mass of European hares collected by shooting and of small rodents sampled by live traps may be slightly greater than that of prey eaten by fox, the values provide a point of reference. We used a wet/dry conversion

factor of 0.30 to obtain dry weight (Golley et al. 1965; Moors 1977). We assigned an average caloric value of 23.4 kJ/g dry weight for both European hares and small rodents. This is generally consistent with data from other sources. Cummins and Wuycheck (1971) determined average caloric value of vertebrates to be 23.46 kJ/g of dry weight, Myrcha (1968) found European hare to have 23.79 kJ/g dry weight, and Wijnanetis (1984) showed Microtus to have 23.43 kJ/g of dry weight.

Because digestion or metabolism is not completely efficient, we estimated utilization efficiency. We calculated apparent net energy available for maintenance and production requirements by multiplying gross energy of food ingested by an apparent digestible energy coefficient (0.90), an apparent metabolizable energy coefficient (0.90), and an apparent net energy coefficient (0.75) (see Robbins 1983). We used the inverse of the preceding calculations to determine the wet weight of protein and the number of European hares or small rodents needed to meet metabolic rates equivalent to 200 to 400% of BMR.

RESULTS AND DISCUSSION

Although grey and culpeo fox recently diverged, they show substantial character divergence in both size and morphology (Wayne et al. 1989). These differences imply the two species have experienced strong selection pressure through competition for resources and space. The intensity of this competition is potentially still strong because both species feed on the same food types and can use similar habitats (see Sections 2-3). Because of culpeo's larger size and greater aggressiveness (culpeo fox have been observed attacking domestic dogs and a Geoffroy's cat (Felis geoffroyi; Johnson and Franklin 1991), we assumed for this discussion that culpeo fox was the dominant species. If culpeo fox is the dominant species, especially where sympatric, grey fox distributions would be influenced strongly by culpeo fox, and culpeo fox distribution would be limited by some factor other than grey fox.

Energy requirements (200 to 400% of BMR) calculated for culpeo fox were 300 to 400% greater than those of grey fox (Table 1). To meet these predicted daily requirements, male and female grey fox need 0.12-0.27 European hares or 7-17 small rodents, compared with 0.4-1.2 European hares or 26-70 small rodents needed to meet the needs of culpeo fox. A 3350-g European hare contributes 33,380 kJ, and the average 40-g small rodent contributes 397.5 kJ to the energy intake of fox. Energy deposition in females during pregnancy is 29.3 kJ/day

for grey fox and 54.4 kJ/day for culpeo fox. Milk output at peak lactation is 2377 kJ/day, or 380% of BMR for grey fox, and 4502 kJ/day, or 210% of BMR, for culpeo fox.

The accuracy of these predicted energy requirements depends heavily on the verity of the equations and values used, and on extrapolation from studies on other species. Because of their recent development, McNab's (1986) equations for determining BMR on the basis of body mass and food habits have had limited use, but the relationships have been corroborated by others (Hayssen and Lacy 1985; Elgar and Harvey 1987). At the very least, the well accepted relationship between BMR and body mass supports the greater energy requirements of culpeo over grey fox. The general reliability of the final figures, however, is supported by Huegel and Rongstad's (1985) finding that coyotes eat 10% of their weight per day, equivalent to the 8-12% found here for energy requirements of 400% of BMR.

At peak lactation, females require a large proportion of the energy they can theoretically produce at maximum sustained working levels. Evidence suggests a negative correlation between average metabolic rate and longevity (Boddington 1978; Lindstedt and Calder 1981), so animals are not expected to maintain maximum metabolic rates outside the reproductive period (Sandell 1989). Therefore, maximum energy requirements calculated here (400% of BMR) probably are most applicable

during birthing season, although culpeo fox will have proportionally greater energy requirements than grey fox throughout the year. Also, because of their greater total energy expenditure for the same level of activity, culpeo fox will reach a critical threshold of energy expenditure sooner as prey energy density declines than will grey fox (Norberg 1977).

The different number of individuals of different prey species needed to meet daily energy requirements of the two fox species has important ecological implications. Efficient foraging and a high density of small rodents would be necessary for culpeo fox to capture the 11 to 15 small rodents needed to meet its minimum daily energy demands. But, only a small fraction of a European hare is needed to meet these energy requirements and, even if fox are preying primarily on smaller, subadult European hare, the size difference between small rodents and European hares would still be substantial. Unless small-rodent densities are very high, culpeo fox should not be able to persist in areas with low European hare densities. Culpeo fox in Torres del Paine National Park would thus be dependent on European hare as prey, and their distribution would be determined by European hare availability.

These results are congruent with field observations at Torres del Paine National Park. If we assume that the much

larger culpeo fox is dominant and is capable of displacing grey fox, then culpeo fox should be found wherever there is appropriate habitat and prey availability, especially where these are available during the breeding season. In Torres del Paine, culpeo fox are distributed only in areas with relatively high densities of European hares (86.6 ± 30.0 (SE) European hares/km^2; see Section 2). Also, in some areas of the Park where culpeo fox were once common (Abello 1979), a near disappearance of European hare has been accompanied by the replacement of culpeo fox by grey fox (W. L. Franklin personal observation).

The energy requirements of culpeo fox, therefore, suggest that its distribution in Torres del Paine National Park, where it is sympatric with the grey fox, is determined in part by the distribution of the European hare. Grey fox, with a more diverse diet, including beetles and berries, and with lesser energy requirements, would be distributed in areas that do not have the prey base to support the culpeo fox. Because prey availability may be related to habitat characteristics, fox distributions also may correlate with, but not be determined directly by, habitat distribution.

Predictions of Geographic Distribution

Projected further, this analysis leads to several predictions

on the geographic distributions of grey and culpeo fox in the absence of strong human pressures. First, culpeo fox will occupy areas with prey densities that allow them to meet their energy needs, and culpeo fox will exclude grey fox from these habitats. Second, grey fox will occupy habitats with food resources insufficient for culpeo fox. Finally, culpeo and grey fox will be sympatric only where "good" and "bad" habitat patches are distributed heterogeneously, or interspersed. In areas where European hare are not common, other species would replace it as the important large-prey item in the culpeo fox diet.

These predictions are corroborated by results of previous studies on culpeo fox food habits. For example, in much of the Argentinean Patagonia, culpeo fox are considered a major predator of sheep, as well as relying heavily on European hare. Culpeo fox may even have increased their range and numbers with the introduction of sheep ranching and European hare in Patagonia (Crespo and DeCarlo 1963; Bellati 1985). In north-central Chile, Meserve et al. (1986) found that culpeo fox feed mainly on two rodents, degus (Octodon degus; 185 g) and chinchilla rats (Abrocoma bennetti; 230 g), the two largest-sized prey in that area. Culpeo fox in central Chile also consumed mainly O. degus and A. bennetti, but in addition preyed heavily on European rabbit (Oryctolagus cuniculus, 450 g) (Jaksic et al. 1980; Simonetti 1986; Duran et al. 1987;

Iriarte et al. 1989). These studies demonstrated that culpeo fox also may show some prey selectivity, consuming larger-sized small-mammals and feeding less on available berries and insects. In contrast, grey fox have been found only in areas with lower densities of medium- to large-sized prey (Simonetti et al. 1984).

Conclusions based on the results of southern Chile should be applied with caution to other areas. The culpeo fox is smaller in the northern portions of its range, and the grey fox increases its size (Fuentes and Jaksic 1979); this may alter the dynamics of their competitive interactions and energetics and, thus, the factors affecting distributions.

It is notable that the diet and distribution of these two species may be dependent on European rabbit, European hare, and domestic sheep, all non-native species. Because these were brought to South America only in the last two centuries, other species had to have been more influential at one time. Before the introduction of European hare into Argentina (Miller and Rottman 1976; Grigera and Rappaport 1983) and European rabbit into central Chile (Housse 1953; Greer 1965), native species such as Patagonian cavies (Dolichotis patagonum), which have a body mass of up to 9-16 kg (Nowak and Paradiso 1983) and plains viscacha (Lagostomus maximus), with adult body masses of 2-8 kg (Weir 1974), may have been important in influencing fox distribution and numbers.

Chinchilla (Chinchilla laniger) and degus (Octodon bridgesi), both now rare, also may have been important prey species. Fox distributions and densities also have probably changed in the last century in response to shifts in land-use patterns and prey availability (Miller 1980).

Although energy models have not been commonly employed to explain carnivore distributions, this analysis demonstrates their potential value. More studies on sympatric populations are needed, ideally incorporating actual measurements of metabolic requirements and models of optimal foraging.

ACKNOWLEDGEMENTS

We thank the Chilean National Forestry and Park Service (CONAF) for their assistance and collaboration. We give special thanks to the personnel of Torres del Paine National Park for their help. Earlier drafts were improved by comments from Michael Behl, Lou Best, William Clark, and Irv Klaas. This study was made possible by grants from the National Geographic Society (Grant No. 3581-87), Patagonia Research Expeditions (Iowa State University), the Organization of American States, the International Telephone and Telegraph Corporation Fellowship Program, and the National Wildlife Federation. This project was conducted under a research agreement (Proyecto Puma) between Iowa State University and the Chilean National Forestry and Park Service. Journal Paper No. J-14871 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2519.

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Table 1. Energy requirements, calculated on the basis of values of basal metabolic rate (BMR), and prey necessary to meet these estimated daily requirements for South American grey (Dusicyon griseus) and culpeo fox (D. culpeus).

	Grey Fox		Culpeo Fox	
	Male	Female	Male	Female
Estimated Daily Requirements				
BMR (kJ/day)	715.5	632	2975	2151
2-4 x BMR (kJ/day)	1431-2862	1264-1468	5950-11900	4301-8602
Needed to Meet Requirements of 2-4 x BMR				
Wet Wt. protein (g)	144-287	127-254	597-1194	432-863
No. European hares	0.04-0.09	0.04-0.08	0.2-0.4	0.1-0.3
No. small rodents	3.6-7.2	3.2-6.4	14.9-29.9	10.8-21.6

GENERAL SUMMARY

The number of sympatric canids in an area appears to be determined by a combination of biogeographical history, human intervention, and environmental diversity and productivity. Temporal partitioning of resources was not very common in canids and no pairs of sympatric canids demonstrated both a high degree of spatial and food overlap. Interactions between sympatric canid species can have a strong impact on canid conservation and management efforts, as demonstrated by changes in canid community structure which have followed a species' range expansion, extirpation, or reintroduction.

Culpeo (Dusicyon culpaeus) and South American grey fox (D. griseus) have comparable ranges in South America, but the factors determining local and geographic distribution are unknown. From 1986 through 1989 44 grey and 19 culpeo fox were monitored using radio telemetry techniques. European hare (Lepus capensis) was the most common vertebrate found in 890 grey fox feces (45%), followed by guanaco (Lama guanicoe; 14%) and Akodon species (13%). European hare accounted for 69% of the prey items and rodent species 20% in 645 culpeo fox feces. Yearly diets were significantly different with ungulates (carrion) and European hare contributing most to the difference. Grey fox were more omnivorous, feeding more on beetles and plants, especially from spring through fall. The index of similarity between fox diets was low (0.14). The

evidence suggests that differences in feeding habits are attributable to differences in food availability in the foxes distribution areas.

Both species were primarily nocturnal. Home ranges of culpeo fox were significantly larger than grey fox, but did not differ between sexes or among seasons. Home ranges of grey and culpeo fox were interspersed in a mosaic-like arrangement, but did not overlap. There were significant differences between fox use of habitat types and cover density categories. Grey fox were located significantly more in upland shrub transition habitat and in areas of medium habitat-density. Culpeo fox were found significantly more in thickets of trees and in areas of high habitat-density. Habitat use was related to availability. Interference competition by culpeo fox or exploitation competition may have been important in determining fox distribution in these distinct habitats. Based on fox energy requirements, it seems that the distribution of grey and culpeo fox in southern Chile is determined in part by the distribution and density of the European hare.

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